

1997

Effects of microhabitat characteristics and spatial scale on recruitment and adult abundance in Caribbean reef fishes.

Nicholas. Tolimieri
University of Windsor

Follow this and additional works at: <http://scholar.uwindsor.ca/etd>

Recommended Citation

Tolimieri, Nicholas., "Effects of microhabitat characteristics and spatial scale on recruitment and adult abundance in Caribbean reef fishes." (1997). *Electronic Theses and Dissertations*. Paper 1861.

This online database contains the full-text of PhD dissertations and Masters' theses of University of Windsor students from 1954 forward. These documents are made available for personal study and research purposes only, in accordance with the Canadian Copyright Act and the Creative Commons license—CC BY-NC-ND (Attribution, Non-Commercial, No Derivative Works). Under this license, works must always be attributed to the copyright holder (original author), cannot be used for any commercial purposes, and may not be altered. Any other use would require the permission of the copyright holder. Students may inquire about withdrawing their dissertation and/or thesis from this database. For additional inquiries, please contact the repository administrator via email (scholarship@uwindsor.ca) or by telephone at 519-253-3000ext. 3208.

INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

**SPATIAL SCALE ON RECRUITMENT AND ADULT ABUNDANCE
IN CARIBBEAN REEF FISHES**

by
Nicholas Tolimieri

A Dissertation
Submitted to the Faculty of Graduate Studies and Research
through the Department of Biological Sciences
in Partial Fulfillment of the Requirements for
the Degree of Doctor of Philosophy at the
University of Windsor

Windsor, Ontario, Canada

©1997 Nicholas Tolimieri

The author has granted a non-exclusive licence allowing the National Library of Canada to reproduce, loan, distribute or sell copies of this thesis in microform, paper or electronic formats.

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque nationale du Canada de reproduire, prêter, distribuer ou vendre des copies de cette thèse sous la forme de microfiche/film, de reproduction sur papier ou sur format électronique.

The author retains ownership of the copyright in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

L'auteur conserve la propriété du droit d'auteur qui protège cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

0-612-30297-0

Canada

Patchiness and scale are essential components in the study of ecology. An important question for ecologists is how these two factors interact to influence the distribution and abundance of species and the structure of assemblages or communities. Specifically, do processes that function at small spatial scales within patches influence population distribution among patches at larger spatial scales?

Benthic marine fishes are excellent models with which to study this question. Adults are closely associated with the substratum and generally spend their entire demersal life within one reef or even one habitat on a reef. However, they produce pelagic larvae that are advected from the reef and recruit to a distant reef. The combination of the patchiness of the reef habitat and the production of pelagic larvae means that different processes can influence the distribution and abundance of a species at different times in the life-cycle and across a number of spatial scales.

In Chapter 2, I examined recruitment in 14 species of Caribbean reef fish. I determine that not all sites (patches of habitat) were equally likely to be replenished (receive recruitment), but that the effect was species specific. Six of the 14 species of fish had spatial patterns of recruitment that were consistent through time, demonstrating that some locations were better supplied with new individuals than other sites. However, not all species recruited well to the same sites, demonstrating that no general recruitment pattern existed for all species. The other 8 species demonstrated highly variable recruitment both in both space and time.

viride, and determined whether large scale recruitment patterns could be explained by small scale microhabitat use. I found that stoplight recruits associate with the coral *Porites porites* at small spatial scales. *Porites* cover predicted the abundance of recruits among 12 sites located in 4 different habitats on the Tague Bay reef, St. Croix, United States Virgin Islands. *Porites* cover also predicted the abundance of stoplight recruits at 10 sites located on 3 different islands during annual censuses conducted at the beginning of August 1991-1994.

In Chapter 4, I examined the influence of pre- and post-settlement processes on recruitment in the stoplight parrotfish more closely. Specifically, I determined the effects of substratum type, conspecific presence, and damselfish presence on settlement and recruitment to 2.0 m² patch reefs. Although stoplights recruited in greater numbers to the coral *Porites* than to the coral *Montastrea*, I found no evidence to suggest that this difference was established by microhabitat choice during settlement. Contrary to these results, stoplights settled in higher numbers to reef that supported resident conspecifics than to empty patch reefs. Persistence was also higher in the presence of conspecifics. Damselfish had no effect on settlement, but they did decrease recruitment. This effect was slightly more pronounced on *M. annularis* patch reefs than on *Porites* patch reefs. These results demonstrate that post-settlement processes can alter initial patterns of settlement such that recruitment may not correlate directly with settlement.

In Chapter 5, I determined whether microhabitat use by 11 species of adult reef fish at small spatial scales predicts their abundance among patches (reefs) at larger spatial

However, only 4 of the species, all damselfish (Pomacentridae), showed correlation between substrata used by individual fishes and abundance among sites. The other species, mostly parrotfish (Scaridae), showed no relationship between microhabitat use at small spatial scales and variation in abundance. These differences appear to be related to how the two families interact with the substratum.

My work shows that processes that function within patches can influence the abundance of a species among patches of habitat. However, the effect is species specific, and for some species, processes related to dispersal among patches are probably more important. Both conclusions hold important implications for managers who wish to create marine reserves to maintain species diversity and to regulate fisheries.

“Whether fate be foul or fair
Why falter I or fear?
What should man do but dare?”

--Sir Gawain of Orkney

“Rough were the waves
and angry sea-beasts had been stirred up.
Then my body-armor, hard-linked, hand-joined,
did me some service against their attack;
my chain-metal war-shirt, worked with gold,
covered my chest. A fierce sea-monster
dragged me down deep, held me on the bottom
in his cruel grip. However, it granted
that my point reached him; I stabbed as I could
with my sharp sword, with battle-thrust killed
the huge sea-beast by my own hand.
Again and again the angry monsters
made fierce attacks. I served them well
with my noble blade, as was only fitting.
Small pleasure they had in such a sword-feast,
dark things in the sea that meant to eat me,
sit round their banquet on the deep sea floor.
Instead, in the morning, they lay on the beach,
asleep from my sword, the tide-marks bloodied
from their deep gashes, and never again
did they trouble the passage of seafaring men
across the ocean. Light came from the east,
God’s bright beacon, and the seas calmed,
till I saw at last the sea cliffs, headlands,
the windy shore. So fate often saves
an undoomed man when his courage holds.
However it was, I chanced to kill
some nine sea-beasts. I never have heard
of a harder night-fight under heaven’s vault,
or a man more oppressed on the ocean streams.
Yet I survived those clutches and lived,
weary in my venture.”

--Beowulf

ACKNOWLEDGMENTS

I thank my committee members Dr. H. MacIsaac, Dr. J. Ciborowski, and Dr. S. Paul for critical comments and suggestions along the way. R. 'the tanner' Nemeth, D. 'Coral Boy' Carlon, 'Dancin' Dan Ha, A. 'Cut-throat' Risk, H. Shaw, M. 'Jesus' Sheehy, L. Woonik, Lucy, Jackie 'the gobie lady' Wilson, D. 'Highlander' Fitch, G. Miller, R. Aaronson, R. Warner, W. Gladfelter, E. Gladfelter, D. Hubbard, C. Gibeault, R. Biche, and E. Kintzing all made my time in St. Croix more fun. N. Marchesi gave me invaluable help during my final field season. Thanks to Diver Bob, Ray and Kathy at the Green Cay Dive Shop for filling tanks, and keeping the Budweiser cold. Thanks to my mom, dad and grandfather for help and support along the way. Francesca Giambartolomei gave me the love and support to finish this project. My greatest thanks go to my advisor Dr. Peter Sale.

ABSTRACT.....	iii
DEDICATION.....	vi
ACKNOWLEDGMENTS.....	vii
TABLE OF CONTENTS	viii
LIST OF TABLES.....	x
LIST OF FIGURES.....	xii

CHAPTER	PAGE
I. INTRODUCTION	
Preamble	1
The life-cycle of marine organisms	3
The importance of patchiness and spatial scale	5
Population dynamics and community structure in marine fishes	7
Patterns of recruitment and adult abundance	10
Factors influencing settlement and recruitment.....	12
Evidence for post-settlement modification of abundance patterns	14
Objectives and scope of the thesis	17
II. RECRUITMENT IN CARIBBEAN REEF FISHES: ARE SPATIAL PATTERNS CONSISTENT THROUGH TIME?	
Abstract.....	19
Introduction.....	20
Materials and Methods.....	25
Results.....	36
Discussion.....	48
III. THE RELATIONSHIP BETWEEN MICROHABITAT, RECRUITMENT AND ADULT ABUNDANCE IN THE STOPLIGHT PARROTFISH, <i>SPARISOMA VIRIDE</i>, AT THREE SPATIAL SCALES	
Abstract.....	62

	Methods.....	85
	Results.....	74
	Discussion.....	81
IV.	THE EFFECTS OF SUBSTRATUM, CONSPECIFICS AND DAMSELFISH ON THE SETTLEMENT AND RECRUITMENT OF THE STOPLIGHT PARROTFISH	
	Abstract.....	92
	Introduction.....	93
	Methods.....	96
	Results.....	102
	Discussion.....	110
V.	INFLUENCE OF MICROHABITAT USE ON THE DISTRIBUTION AND ABUNDANCE OF CARIBBEAN CORAL REEF FISHES AT TWO SPATIAL SCALES	
	Abstract.....	119
	Introduction.....	120
	Methods.....	123
	Results.....	129
	Discussion.....	143
VI.	GENERAL DISCUSSION	153
VII.	LITERATURE CITED	159
VIII.	VITA AUCTORIS	185

	Page
Table 2.1. Recruitment of 40 species of fish recorded from 1991-1994.....	35
Table 2.2. Rotated component loadings for principle component analysis describing variation among sites in terms of fish recruitment.....	39
Table 2.3. Results of Multivariate analysis of variance on fish recruitment.....	40
Table 2.4. Results of F-tests and variance components on recruitment.....	49
Table 2.5. Results of variance components analysis.....	51
Table 2.6. Rotated component loadings for principal component analysis and r^2 for relationship between recruitment and habitat characteristics.....	53
Table 2.7. Coefficient of variation for recruitment from Sale et al. (1994) and the present study	55
Table 3.1. Persistence of 12 fin-clipped fish on the fore reef slope	75
Table 3.2. Results of ANOVA on stoplight recruitment to different habitats on the Tague Bay reef for 1994 and 1995.....	77
Table 4.1. Results of repeated measures ANOVA on recruitment of stoplight parrotfish to <i>Porites</i> and <i>Montastrea</i> patch reef in the presence and absence of damselfish	107
Table 4.2. Results of two-way ANOVA by size class	108
Table 4.3. Results of MANOVA on parrotfish behavior	116
Table 5.1. Results of contrasts comparing individual species to null data.....	131

use by damselfish and parrotfish on the fore reef	132
Table 5.3. Canonical loadings for discriminant function analysis of small scale habitat	
use by damselfish and parrotfish on the back reef	135
Table 5.4. Preliminary results of stepwise regressions to determine whether microhabitat	
use influenced adult abundance	137
Table 5.5. Correlations between mean adult abundance and live coral cover among the	
13 sites	140
Table 5.6. Correlations between species among sites	143

Figure	Page
Figure 2.1. Fig. 1. Location of study sites.....	26
Figure 2.2a. Mean recruitment of 8 species at 10 sites around the Virgin Islands for 4 years.	37
Figure 2.2b. Mean recruitment of 6 species at 10 sites around the Virgin Islands for 4 years.	38
Figure 2.3. Mean percentage cover of 13 substrata at the 10 study sites	42
Figure 2.4ab. Results of cluster analysis on mean recruitment of 14 species of reef fish used to join 10 sites.....	43
Figure 2.4cd. Results of cluster analysis on mean recruitment of 14 species of reef fish used to join 10 sites.....	44
Figure 2.5ab. Results of cluster analysis on mean habitat characteristics used to join 10 sites..	46
Figure 2.5cd. Results of cluster analysis on mean habitat characteristics used to join 10 sites..	47
Figure 3.1. Location of the study sites	67
Figure 3.2. Abundance of four substratum types in stoplight and null quadrats on the fore reef slope of the Tague Bar Reef	76
Figure 3.3. Recruitment of stoplight parrotfish in four habitats on the	

Figure 3.4. Results of regression analysis showing the relationship between the mean proportional cover of <i>Porites</i> and mean recruitment of stoplight parrotfish in 4 habitats around the Tague Bay Reef.	80
Figure 3.5. Results of regression analysis showing the relationship between the percent cover of <i>Porites</i> and recruitment of stoplight parrotfish at a large spatial scale over four years.	82
Figure 3.6. Relationship between recruitment and adult abundance at 10 sites for <i>Sparisoma viride</i>	84
Figure 4.1. (a) Natural density of stoplight recruits on two substrata at Tague Bay. (b) Total settlement density to the same patch reefs.....	103
Figure 4.2. Settlement of stoplight recruits in the presence and absence of damselfish and at three densities of resident conspecific recruits.....	105
Figure 4.3. Percent change in the density of resident stoplight recruits in the presence and absence of damselfish and at two densities of resident stoplight recruits	106
Figure 4.4. Behavior of stoplight recruits: (a) # of bites per 10 min. (b) # of chases	109
Figure 4.5. Change in the density of stoplight recruits through time.....	111
Figure. 4.6. Change in the density of stoplight recruits through time separated by size class.....	114
Figure 5.1. Location of the study sites around St. Croix	124

Tague Bay	130
Figure 5.3. Plot of the first and second canonical variates describing damselfish microhabitat use on the fore reef.....	133
Figure 5.4. Plot of the first and second canonical variates describing damselfish microhabitat use on the back reef	134
Figure 5.5. Plot of the first and second canonical variates describing parrotfish microhabitat use on the fore reef.....	136
Figure 5.6. Plot of the first and second canonical variates describing parrotfish microhabitat use on the back reef	138
Figure 5.7. Abundance of (a) damselfish and (b) parrot fish at 13 sites around St. Croix, and (c) cover of 8 microhabitat characteristics at the same sites	139
Figure 5.8. Relationship between microhabitat characteristics and abundance for 4 damselfish.	141

Preamble

At the most basic level, all ecologists are interested in the distribution and abundance of organisms in space and time (Andrewartha and Birch 1954; Krebs 1978). We seek to document patterns in species abundance and to understand the processes that are responsible for creating these patterns. When investigating the population ecology of an organism, it is important to keep two factors in mind. First, the biology or life-cycle of the organism is important because it plays a crucial role in determining what types of factors can influence the ecology of the species. Second, it is essential to define the scale at which we are interested because different processes may affect population dynamics at different spatial or temporal scales. Species that live in patchy environments and have dispersive propagules are superb examples of the importance of the interaction between biology and spatial scale.

Marine ecosystems are patchy across several spatial scales, and populations of benthic or demersal marine organisms exist as a series of local populations in an open system (Sale 1991a). Many benthic invertebrate and demersal fishes produce pelagic propagules that disperse from the local population to eventually recruit (successfully establish juveniles in the adult habitat; see below) to a distant benthic population (Thorson 1950; Sale 1980, 1991a,b; Dayton 1985; Doherty and Williams 1988; Roughgarden et al. 1988; Doherty 1991). The distribution and abundance of such organisms is determined by many different factors, some of which operate during the

life-cycle. Populations of benthic marine organisms may or may not be metapopulations in the classic sense (Hanski and Gilpin 1991; Hanski et al. 1995; Man et al. 1995), but they do function under similar constraints concerning dispersal among patches. For these organisms, dispersal among patches is essential to the persistence of each local population and the metapopulation as a whole (Sale 1991b; Hanski and Gilpin 1991). At the same time, it is essential to determine the relative importance of processes that function at small spatial scales, within patches, to the distribution and abundance of the metapopulation at larger spatial scales. The important question we must ask is: How do process and spatial scales interact? Do processes that function within patches at small spatial scales influence the distribution and abundance of organisms among patches at larger spatial scales.

The goal of this work is to examine the relative importance of several factors in influencing recruitment and adult abundance of coral reef fishes across several spatial scales. I start by examining recruitment in a number of Caribbean reef fishes and determine whether spatial patterns of recruitment are consistent throughout time. I then examine possible causes for the patterns that I see. I question whether or not processes like competition, predation and microhabitat use that function at small scales (within patches or at the level of the individual) influence distribution and abundance among patches. Specifically, I determine whether microhabitat use by individual recruits and adults influences the distribution and abundance of these fishes at large spatial scales or among patches of suitable habitat. I also examine whether patterns of microhabitat use

introduction, I review the life-cycle of coral reef fishes, in and the influence of various processes during different stages of the life-cycle.

The life-cycle of marine organisms

A species has a complex life-cycle if it has at least two distinct developmental stages that inhabit different environments or habitats (Roughgarden et al. 1988). In marine organisms, a common pattern is for demersal, sedentary adults to produce pelagic propagules (eggs and/or larvae) that enter the water column and disperse from the local habitat patch (Thorson 1950; Sale 1980, 1991; Roughgarden et al. 1988). This pattern is followed by marine algae (Dayton 1985), barnacles (Gaines et al. 1985; Roughgarden et al. 1988), other benthic invertebrates (Thorson 1950; Yoshioka 1982; Roughgarden et al. 1988; Underwood and Fairweather 1988), and demersal fishes (Ehrlich 1975; Sale 1980; Doherty 1991). Almost all of the fish species on coral reefs produce pelagic larvae with one notable exception (Sale 1980; Doherty and Williams 1988; Leis 1991).

Adult coral reef fishes are closely associated with the substratum, which they use for shelter, food and nesting sites (Thresher 1973; Jones 1991; Hixon 1991; Sale 1991a). They are often territorial and utilize small home ranges (Sale 1971; Thresher 1973; Kaufman 1977; Clifton 1989, 1990, 1991). The length of the larval stage lasts from 9-100 days depending on the species, and larvae can disperse over very long distances (Sale 1980; Leis 1991). As larvae disperse, they develop in the water column away from the reef. Although workers have generally considered larvae to be passive particles, there is

water column to some extent (Thorrold et al. 1994c; Castro and Cowen 1994; Sponaugle and Cowen 1996), making broad pre-settlement decisions regarding habitat selection (Doherty et al. 1996), and are capable of swimming for considerable time and distances against currents (Stobutzki and Bellwood 1994, in press). After developing in the plankton, these individuals move from the water column back to the adult habitat--a process termed **settlement**. Larvae usually possess a number of morphological characteristics such as lack of pigmentation, numerous fin and head spines, and large eyes, which presumably are adaptive for the pelagic stage (Leis 1991). Settlement is accompanied by metamorphosis from the pelagic morphology to the demersal form.

Settlement is difficult to measure directly for reef fishes. Instead, ecologists often quantify **recruitment**. Recruitment is the processes by which populations of fishes on coral reefs are replenished. Recruitment when quantified refers to the abundance of recently settled fishes on the reef (Keough and Downes 1982; Levin 1991; Caselle and Warner 1996). Recruits have been on the reef from one day up to several months, and the pattern of recruitment can be altered from the initial settlement pattern by post-settlement, benthic processes. Where settlement and recruitment are seasonal, recruitment corresponds with the abundance of young-of-the-year (YOY) individuals (Doherty and Fowler 1994a,b; Williams et al. 1994). However in some areas, such as the Virgin Islands, settlement and recruitment can occur year round. In such cases, recruitment does not represent YOY abundance but is understood to refer simply to recently settled fishes. Recruitment has been shown to be an important factor in the

Minchinton and Scheibling 1991) to bryozoans (Yoshioka 1982) and to reef fishes (Williams 1980; Doherty 1983; Victor 1983; Jones 1990; Doherty and Fowler 1994a,b).

The importance of patchiness and spatial scale

Like many environments, coral reefs are patchy across a number of spatial scales (Sale 1991b). Individual coral heads of various species are scattered about reefs at a spatial scale of meters. Monospecific stands of the same species of coral can cover areas that range from 10's of m^2 to 100's of m^2 in area on a reef. Reefs can have several habitat zones (fore reef/back reef) with different vertebrate and invertebrate communities, as well as different abiotic environmental conditions. These reefs are distributed around islands and the ocean at scales of kilometers to tens or hundreds of kilometers. At scales of hundreds to thousands of kilometers, groups of reefs are scattered about the tropical seas in different regions. For the purpose of this thesis, I define small spatial scale as a scale of meters, usually that of interest to an individual fish, although I will also use 'small scale' to refer to the abundance of fishes on small patch reefs (one to several m^2 in area). I use medium scale to refer to locations along the same reef, often in different habitats. These locations can be separated by 100's of meters to several kilometers. A site is a location at which I did a series of 30 m^2 transects. The minimal area of a site is between 480 - 960 m^2 (depending upon how many transects were done) but is actually at least 3 - 4 times that size since transects were separated by at least several meters. Large scale reflects the abundance of populations among distant sites not necessarily on the

of suitable habitat that has definite physical edges. When I refer to the importance of benthic processes within and among patches, I refer to patches are isolated such that juvenile and adult fishes probably do not move between them to any great extent (Southwood 1977).

The most important consequence of the two part life-cycle and the patchiness of the environment is that these species exist in open, non-equilibrial systems (Sale 1991b). The reproduction that occurs in a patch of habitat or on a reef is exported in the form of pelagic larvae, and the replenishment of local, demersal populations depends upon the arrival of larvae from external sources. The patchiness of the coral reef environment means that different processes can affect the distribution and abundance of reef fishes at different spatial scales and at different times in the life-cycle. Prior to settlement, larval growth and survival in the plankton, oceanic currents, and stochastic weather events can determine the availability of larvae at a number of spatial scales. During settlement, larval behavior and interactions with resident fishes can affect where larvae settle at medium and small spatial scales. Finally, once fish are on the reef, processes like competition and predation may influence the abundance of fishes at small spatial scale.

Historically, reef fish ecologists first focused on the role of post-recruitment, equilibrial processes (i.e., competition among adults) as the major factors in the regulation of populations and communities (Smith & Tyler 1972, 1973, 1976; Goldman and Talbot 1976; Smith 1978; Jones 1991). Through time, however, the focus has shifted to include the full scale of processes that are potentially important during the various

Williams 1988; Jones 1990). Below, I review the various models that have been put forth for reef fish population and community dynamics. I then discuss in more detail the factors that have been shown to be important during different stages in the life-cycle of reef fishes and the spatial scales at which they function.

Population dynamics and community structure in marine fishes

Initially, ecologists believed that intra- and interspecific competition during the post-settlement stage were the most important processes structuring assemblages of coral reef fish and the populations within them. The **Competition Model** assumes that recruits are abundant and that resources, usually space, are limiting. Populations and communities are in equilibrium, and as long as resources do not change, population levels should remain fairly constant (Smith 1978; Goldman and Talbot 1976; Jones 1991). Community structure (composition and abundance of various fish species) is determined by interspecific competition and other biotic interactions.

The Lottery Hypothesis (Sale 1974, 1977, 1978) was the first departure from an entirely equilibrial view of population dynamics and community structure for reef fishes. It proposes that larvae are plentiful and that space, which all species are theoretically capable of obtaining and defending, is limited. Variation in recruitment determines community structure because this variation determines which species are present to fill the gaps produced by adult mortality. The lottery hypothesis is a non-equilibrial model because stochastic variation in recruitment (not competition) controls representation in

size (total number or biomass of fishes). Although the Competition model and the Lottery Hypothesis were both proposed as community models their basic principles are easily applied to the population level. The lottery hypothesis has obvious connections to gap formation in forest communities (Hubbell 1979; Runkle 1981, 1982; Brokaw 1985a,b), and to a lesser extent, the role of gaps and disturbance in rocky intertidal communities (Sousa 1979a,b; Paine and Levin 1981).

The **Recruitment Limitation** model (Williams 1980; Doherty 1981, 1982, 1983) was derived from the Lottery Hypothesis, and marked a complete departure from equilibrial ideas about community structure and population dynamics. It is a population model, but its ideas are readily applied to community dynamics as well. It postulated that larval supply is normally too low to allow adult populations to achieve or exceed the carrying capacity (Williams 1980; Doherty 1982, 1983; Victor 1983, 1986). Mortality is density-independent, and the distribution and abundance of adults reflects prior settlement rates rather than density-dependent, post-settlement processes because resources are never limiting. Victor (1983, 1986) identifies this situation as **primary recruitment limitation** to distinguish it from **secondary recruitment limitation**. Under secondary recruitment limitation, the supply of larvae is substantial enough that competition among adults could occur. However, benthic mortality of newly settled fishes is intense and reduces replenishment to such an extent that adults do not compete. This mortality may be density dependent and lead to recruitment bottlenecks, but mortality need not be density-dependent. Benthic mortality may also alter the pattern of

settlement. Adult populations are below carrying capacity, and competition among adults does not structure the assemblage of fishes on the reef. The distinction between primary and secondary recruitment limitation was important because one implies that post-settlement processes are entirely unimportant, while the second implies that they are important only during the earliest stages of the benthic life of the fish. Competition is still unimportant in both models. Secondary recruitment limitation is related to the predation model.

The **Predation Model** proposes that predation on new recruits, juveniles and adults is so intense that competition for non-shelter resources does not occur, and post-settlement mortality due to predation limits adult abundance (Hixon 1991; Hixon and Beets 1989, 1993; Carr and Hixon 1996). Population size is modified by post-settlement processes, but post-settlement competition for non-shelter resources is weak. Competition for shelter related resources may or may not be important.

Although these models for population and community regulation were developed as separate concepts, they are not mutually exclusive, and there is evidence that both pre-settlement and post-settlement factors are important in determining the distribution and abundance of coral reef fishes. In the next sections, I provide a review of recruitment patterns, factors that affect settlement and recruitment, and post-settlement processes that can alter the initial pattern of abundance set up by recruitment processes.

Although exceptions do occur, seasonal variation in recruitment is common, with most of the recruitment occurring during the summer months (Doherty and Williams 1988; but see McFarland et al. 1985; Booth and Beretta 1994). Recruitment usually occurs in pulses lasting a few days up to a week (Russell et al. 1977; Doherty and Williams 1988; Robertson 1992). Pulses are often coherent temporally over several kilometers (Victor 1984). Victor (1984) suggested that this coherence was due to the movement of a patch of larvae through the area via ocean currents. Other authors have pointed out that the timing of recruitment pulses is often related to lunar cycles and the spawning cycles of adult fishes (Doherty 1983, 1987, Robertson 1988c, 1992; Caselle and Warner 1996).

The abundance of recruits arriving on a reef is highly variable both spatially and temporally (Doherty and Williams 1988; Doherty 1991). Fowler et al. (1992) examined variation in the recruitment of *Chaetodon rainfordi* on the Great Barrier Reef at three spatial scales over three years. At a geographic scale that spanned a latitude of approximately 1,000 km, recruitment was consistently higher in three southern regions than in the two northern ones, but the overall intensity of recruitment varied from year to year. Within this overall pattern, however, there were statistical interactions between reefs and years and between regions and years indicating the presence of stochastic modification of more general recruitment patterns. Within a region (a group of reefs separated by 70 km), recruitment varied over years, reefs, and places on reefs. At this scale there was no interaction between reefs and years. Therefore, over 3 years, certain

recruitment varied from year to year. However, within reefs, recruitment intensity differed between years, and sites, and there was a significant interaction between years and sites suggesting the influence of stochastic processes at this scale. Indeed, most studies have found recruitment to be stochastic at small scales and variable across years (Doherty and Williams 1988; Fowler et al. 1992).

Recruitment may be variable, but how does this variation affect adult populations? If sizes of adult populations are primarily influenced by density dependent processes, variation in recruitment above some threshold may be unimportant. Several authors have demonstrated that low levels of recruitment can limit population sizes (Williams 1980; Doherty 1982, 1983; Victor 1983, 1986). Williams (1980) removed pomacentrids from patch reefs and monitored recruitment to these reefs. Some reefs had not recovered to original population levels after two years, and he suggested that recruitment was not high enough to saturate these populations. Doherty (1982) transplanted juveniles of *Pomacentrus flavicauda* and *P. wardi* to patch reefs. Densities of fish at the end of the experiment reflected the starting densities, suggesting that mortality was independent of density. Victor (1986) found that the settlement rate of the bluehead wrasse, *Thalassoma bifasciatum*, was correlated with larval supply, and that adult populations at several sites reflected larval supply and settlement rate. Victor concluded that larval settlement in these cases was too low to "saturate the habitat in terms of space and food" (Jones 1986). The strongest evidence of recruitment limitation to date comes from Doherty and Fowler (1994a,b). They found that recruitment over a

on patch reefs in lagoons separated by 10's of kilometers.

Factors influencing settlement and recruitment

Variation in recruitment among locations is usually attributed to variability in the abundance of pre-settlement fish (Hjort 1914; Victor 1984, 1986; Doherty 1987, 1988; Doherty and Williams 1988; Pitcher 1988; Fowler et al. 1992; Sponaugle and Cowen 1994). The temporal availability of larvae is stochastic and probably influenced by temperature, weather, and survival of larvae in the plankton. Spatial variation in larval supply has been attributed to oceanic currents (Sale 1980; Victor 1986; Doherty and Williams 1988; Castro and Cowen 1994; Sponaugle and Cowen 1996; Caselle and Warner 1996), and local tidal and weather conditions (Shenker et al. 1993). For example, Victor (1986), working with the bluehead wrasse, *Thalassoma bifasciatum*, found that the intensity of recruitment among sites within a 1000 km² area was correlated with both distance from shore and the presence of larvae in the water column at these sites. At a smaller scale of 1 km², recruitment was highly variable suggesting the involvement of stochastic processes. Recently, Caselle and Warner (1996) provided evidence that suggested that island scale patterns of recruitment of *T. bifasciatum* around St. Croix were also related to current patterns. Since their sites were chosen to be very similar in habitat and microhabitat characteristics, their sampling design minimized any influence of these factors on recruitment.

well as the presence of resident fishes influence rates of settlement for some fishes (Sale et al. 1984a; Shulman 1984; Sweatman 1985, 1988; Carr 1991; Levin 1991, 1993, Booth 1992; Wellington 1992; Tolimieri 1995). In an attempt to explain the distribution of the adults of two Caribbean damselfish, Wellington (1992) examined the settlement to the fore reef and back reef of Tague Bay, St. Croix, USVI. Settlement patterns matched the pattern of adult abundance. Sale et al. (1984a) recorded microhabitat use by newly settled fishes on 20 patch reefs. Some species showed strict preferences for certain substrata. For example, *Dascyllus aruanus* was associated with live coral. The abundance of other species was related to factors such as height on the reef (*Pomacentrus wardi*), angle of the substratum (*P. wardi*), and the proportion of living coral (scarids). Shulman (1984) found that shelter size and quantity affected the settlement of juvenile fishes to artificial reefs built from conch shells. Sweatman (1985) showed that the presence of adult *D. aruanus* and *D. reticulatus* on standard coral units (SCU's) increased the settlement of conspecific larvae. Conversely, these adults reduced the settlement of all the other species that settled in high enough numbers to permit statistical analysis. In a later experiment, Sweatman (1988) showed that *Dascyllus* larvae used chemical cues to locate adults. Booth (1992) found similar results for the domino damselfish, *D. albisella*, which settled in greater numbers with conspecifics.

Studies on temperate reef fish have yielded similar results (Carr 1991, 1994a; Levin 1991, 1993, 1994a,b; Levin and Hay 1996). Levin (1991) found that microhabitat characteristics could be used to predict the presence or absence of recruits of the

microhabitat characteristics were not important in explaining variation in the abundance of the recruits within these quadrats. Instead, variation in abundance was explained by the availability of food within these quadrats (Levin 1994a). Later experiments (Levin 1993) demonstrated that larval settlement was affected by macroalgal habitat characteristics, but conspecifics had no effect on settlement.

Evidence for post-settlement modification of abundance patterns

After settlement has established the initial pattern of recruit abundance, post-settlement processes such as competition (Jones 1986, 1987a,b, 1988a; Forrester 1990, 1995; Booth 1995), predation (Hixon 1986, 1991; Hixon and Beets 1989, 1993; Shulman and Ogden 1987; Carr and Hixon 1995), or other benthic processes (Tupper and Hunte 1994; Pfister 1996; Schmitt and Holbrook 1996) can modify these patterns. If post-settlement mortality is high, it may preclude any relationship between recruitment patterns and adult abundance (Shulman and Ogden 1987, Robertson 1988a; Pfister 1996). Factors such as food limitation (Jones 1986; Forrester 1990; Clifton 1995), interaction between shelter and predation (Hixon 1991; Hixon and Beets 1989, 1993; Shulman and Ogden 1987), and social interactions (Sale 1972a; Doherty 1982; Jones 1987a,b, 1988a; Forrester 1990) affect growth rates and survivorship during the post-settlement stage.

Variation in growth rate is important because it can stagger the entrance of fishes into the adult population (Doherty 1983; Thresher 1985; Gladstone and Westoby 1988; Jones 1987a; Forrester 1990; Booth 1995). Intraspecific competition among reef-fishes

the presence of adults (Doherty 1982, 1983; Jones 1987a,b; 1988a, Forrester 1990, 1995; Booth 1995). For some species, this variation in growth is caused by complex behavioral interactions involving access to food (Forrester 1990, 1991). Both Jones (1986) and Forrester (1990) saw increased growth rates when supplemental food was provided. For example, Forrester (1990) found that although supplemental food increased the growth rate of juvenile *Dascyllus aruanus*, it did not do so in the presence of conspecific adults. The presence of adults decreased the growth rates of juveniles, but at the same time, it increased the survival of these juveniles. Forrester attributed the reduced growth in the presence of adults to the behavior of the adult fishes. These fish fed farther "upstream" from the coral heads than did juveniles, and therefore, had first access to higher quality plankton. Because adults strayed farther from the reef during feeding bouts, predator vigilance of the group may have been increased, accounting for the higher survivorship of juveniles in the presence of adults.

Habitat and microhabitat characteristics also influence the post-settlement mortality of reef-fishes. Work by Hixon and Beets (1989, 1993) and Carr and Hixon (1995) strongly suggests that this effect is due to the influence of predation, although food availability may be important for some species (Clarke 1992). The mortality rates of new recruits can be affected by (1) general habitat characteristics, such as the broad structural differences between fore reef and back reef (Wellington 1992); (2) microhabitat characteristics such as coral type and shelter size (Jones 1988a; Hixon 1989, 1993); and (3) depth (Jones 1988a). For example, Wellington (1992) compared the survival of

Croix, USVI. He found that *S. leucostictus* recruits experienced higher survival on the fore reef than on the back reef, while the opposite was true for *S. variabilis*. Jones (1988a) examined the effects of intra- and interspecific competition and coral type in a multi-factorial experiment. His results showed that coral type had a much larger influence on survival of juvenile *Dascyllus aruanus* and *Pomacentrus amboinensis* than did competition. Survival of *P. amboinensis* was also affected by depth (Jones 1986).

Mortality rates can differ between locations (Aldenhoven 1986) and among habitats (Doherty 1980; Jones 1990; Wellington 1992). Areas with more shelter or more complex topography tend to support greater populations of fishes, suggesting that predation may be an important interacting factor (Luckhurst and Luckhurst 1978; de Boer 1978; Shulman 1984; Hixon and Beets 1989, 1993). Hixon and Beets (1993) examined fish assemblages on artificial reefs constructed from concrete blocks with different numbers of holes and sizes of holes. "Prey fish" were more abundant on reefs with hole sizes that were closest to the fish's body size. They also observed "extreme type III survivorship curves" on reefs with many predators. In addition they observed a negative relationship between the abundance of predators among reefs and the prey-species richness of those reefs. Since early benthic mortality of reef fishes is often high (Shulman and Ogden 1987; Robertson 1988a; Jones 1991), small changes in mortality rates may have profound impacts on adult populations in the absence of density-dependence.

The goal of this work was to examine the relative importance of several factors in influencing recruitment and adult abundance in coral reef fishes across several spatial scales. I question whether or not processes that function at small scales (within patches) can influence distribution and abundance among patches at larger spatial scales. Specifically, I determine whether small scale microhabitat use influences the distribution and abundance of these fishes at large spatial scales or among patches.

In Chapter 2, I examine patterns of recruitment in 14 species of Caribbean coral reef fish at two spatial scales: islands and sites within islands. I examine spatial and temporal patterns of recruitment and question whether some species have spatial patterns of recruitment that are consistent through time. In Chapter 3, I study the stoplight parrotfish, *Sparisoma viride* (one of the species that had a spatially consistent pattern of recruitment through time), and determine the importance of microhabitat use by that species in establishing this consistent pattern. I start by determining what microhabitat characteristics influence the distribution of individual recruits within patches (small scale). I then ask whether the abundance of substrata important at the small spatial scale predicts recruitment among sites across several larger spatial scales: sites in different habitat around the same reef, and sites on different islands. In Chapter 4, I continue to focus on *S. viride* and determine whether the pattern of microhabitat use at small spatial scales is determined by pre- or post-settlement processes. In Chapter 5, I return to examining several species and continue along the theme of within patch substratum use versus large scale abundance. Here, I examine adult microhabitat use by 11 species of

associate with within patches determine their abundance among patches.

My results demonstrate that recruitment patterns can be consistent through time even at large spatial scales. Microhabitat use by individual fish at small scales predicts recruitment for the stoplight parrotfish across a number of scales from the distribution of individual fishes within a patch of habitat to the abundance of recruits at 10 sites on 3 different islands located up to 70+ km apart. Microhabitat use by stoplight recruits appeared to be due to post-settlement processes involving movement or differential mortality. Microhabitat use by adults also predicted adult abundance at large scales, but the relationship was weaker and not present for all species. I conclude that processes that function at small spatial scales within patches can be important in explaining variation in distribution and abundance at large scales.

Abstract

Many benthic marine invertebrates and demersal fishes produce dispersive, pelagic larvae. Large fluctuations in recruitment, the addition of individuals to the benthic population following settlement, are common both in space and time, and these fluctuations can influence population size and community dynamics. In this report, we examine the recruitment of 14 species of Caribbean reef fishes over 4 years at 10 sites in the waters around three islands in the US and British Virgin Islands: St. Croix, St. John, and Virgin Gorda. Our intent was to determine 1) the extent of spatial and temporal variation in recruitment, 2) whether there were spatial patterns that were consistent through time, 3) whether there were correlations among species with regards to recruitment, and 4) whether substratum characteristics influenced recruitment.

MANOVA and univariate F-tests revealed significant spatial and temporal variation in recruitment for all 14 species investigated. However, we detected two general types of recruitment patterns. Six of the 14 species showed recruitment patterns that were spatially consistent through time. Variance components indicated that variation among sites within years accounted for most of the variance, and concordance analysis

¹ This chapter was submitted to J. Exp. Mar. Biol. Ecol. as Tolimieri N, Sale PF, Nemeth RS & KB Gestring, and is therefore written in the first person plural.

presented recruitment patterns that were highly variable both spatially and temporally. A substantial proportion of the variance was due to the interaction between sites and years indicating that the pattern of recruitment varied among sites in different ways each year.

Principal components analysis indicated some relationships among species in terms of recruitment. For example, all planktivorous species loaded on the same component. We found only weak evidence that spatial variation in recruitment was correlated with variation in microhabitat characteristics (ca. 20% of the variation in recruitment was correlated with microhabitat characteristics). These results indicate that deterministic processes may dictate the pattern of recruitment among sites for some species, while other species have much more variable recruitment.

Introduction

Metapopulation theory attempts to explain the large scale distribution of local populations among patches of suitable habitat in terms of the extinction rate within patches and the migration rate among patches. Populations of benthic marine organisms may or may not be metapopulations in the classic sense (Hanski and Gilpin 1991; Hanski et al. 1995; Man et al. 1995), but they do function under similar considerations concerning dispersal among patches. Marine ecosystems are patchy across several spatial scales and populations of benthic or demersal marine organisms exist as a series of local populations in an open system (Sale 1991b). For these organisms, dispersal among patches is essential to the persistence of each local population and the metapopulation as a whole (Sale 1991b; Hanski and Gilpin 1991). Dispersal among patches is undertaken

Recruitment includes settlement plus a short period of time one the reef and is analogous to immigration. Once an individual has arrived in a local patch, it will normally spend the remainder of its life within that patch (Sale 1980; Roughgarden et al. 1988). Unlike immigration, recruitment is the sole source of replenishment for the local population and variable recruitment may have strong effects on local population size.

Basic metapopulation models assume that dispersal is random and the chance of successful immigration to a patch (here recruitment) is the same for all patches (Hanski and Gilpin 1991). In marine systems, large scale dispersal of larvae is strongly influenced by current regimes so we might expect that dispersal and subsequent recruitment might be more predictable and uneven among patches (Shanks 1983; Victor 1983, 1986; Kingsford and Choat 1986; Leis 1991; Sponaugle and Cowen 1996). However, recruitment is often highly variable in space and through time presumably due to high and variable larval mortality and stochastic weather patterns (Sale 1980, 1991b, Underwood and Denley 1984, Caffey 1985, Doherty and Williams 1988, Roughgarden et al. 1988; Doherty 1991).

Work on both benthic invertebrates and demersal fishes has shown that recruitment variation can influence the distribution, abundance and dynamics of populations and communities (Coe 1953, 1956; Sale 1977; Doherty 1983; Yoshioka 1982; Victor 1983, 1986; Underwood and Denley 1984; Gaines and Roughgarden 1985; Gaines et al. 1985 Roughgarden et al. 1988; Hughes 1990; Jones 1990; Raimondi 1990; Minchinton and Scheibling 1991; Carr 1994a,b; Peterson and Summerson 1992; Doherty and Fowler 1994a,b; Peterson et al. 1996). Therefore, it is important to understand how

through time.

Nearly all of the demersal fishes that inhabit coral reefs produce pelagic larvae, which spend 14-100 days in the plankton (depending on the species) prior to undergoing metamorphosis and settling to the reef habitat (Sale 1980, Doherty and Williams 1988, Leis 1991). Reef fish are generally considered to exist in open populations, but there is evidence that some lagoon populations of some species may exhibit more closed systems (Leis 1994). Settlement is more difficult to measure directly for demersal fishes than for benthic invertebrates. Instead, ecologists often measure recruitment, which is operationally defined as the addition of a new cohort to the benthic population at a time defined by the ecologist, usually when first censused after settlement (Keough and Downs 1982; Connell 1985). In the context of this study, we define ‘the assemblage’ as the recruits of all species of fish that recruited in large enough numbers to warrant inclusion in statistical analyses. ‘Assemblage-level recruitment’ refers to the recruitment of all species considered at the same time in a multivariate variate context. For example, at the assemblage level, two sites might receive similar assemblage level recruitment to each other within years even though the abundance of individual species varies from one year to the next. We considered a spatial pattern to be temporally consistent if the ranking of sites was the same or very similar from year to year. A site was a permanent location at which a set of haphazard transects was sampled.

Recruitment can strongly affect adult population size, distribution, and age structures of coral reef fishes (Doherty 1982, 1983, Victor 1986, Warner and Hughes 1988, Doherty and Fowler 1994a,b, see also Hjort 1914, Bailey 1981, for temperate

limited. That is, adult abundance is determined by the intensity of recruitment and not by processes operating among adults on the reef (Doherty 1981, 1983, 1991, Victor 1986, Doherty and Fowler 1994a,b). This conclusion is supported by both small spatial-scale, manipulative studies conducted on patch reefs (Williams 1980, Doherty 1982, 1983), and by larger-scale observational studies covering many kilometers (Victor 1983, 1986, Doherty and Fowler 1994a,b). There is also abundant evidence that post-settlement processes can affect growth and mortality of juvenile fish (Jones 1987a,b, 1988a; Hixon and Beets 1989, 1993, Forrester 1990, Levin 1993, Booth 1994, Robertson 1996). However, the importance of these post-settlement processes varies with the level of recruitment (Connell 1985, Menge and Sutherland 1987, Jones 1990). In theory, when recruitment is low in relation to resources, competition should be unimportant. Other post-settlement processes, such as predation, may be important regardless of the relationship between recruitment and resources. When recruitment is high, biotic interactions among individuals on the reef become important.

Because recruitment can affect population size and community dynamics it is important to know not only whether recruitment varies, but whether the spatial patterns of recruitment, both within and among sites, are consistent through time. The presence of spatial patterns that are consistent through time suggests the influence of deterministic processes in establishing these patterns (Fowler et al. 1992). Likewise, although populations and communities of reef fishes may be recruitment-limited, they may still be somewhat predictable in structure if spatial patterns in recruit abundance are consistent through time. For example, if recruitment is limiting, we might expect adult populations

recruitment is low. Again, competition may be important only when recruitment is high. Alternatively if spatial patterns vary substantially from year to year, adult abundance and community structure may be less predictable (Sale et al. 1984a).

Patterns of spatial and temporal variation in recruitment of reef fishes at larger spatial scales have been examined by several researchers on the Great Barrier Reef (Williams and Sale 1981, Eckert 1984, 1985, Sale et al. 1984b, Doherty 1987, Milicich et al 1992, Fowler et al. 1992, Doherty and Fowler 1994a,b). This work has shown that recruitment is highly variable but that there are also some consistent patterns (Sale et al. 1984, Doherty 1987, Fowler et al. 1992). Similar recruitment information from the Caribbean is less abundant, or has focused on smaller spatial scales or larval supply questions (Shulman 1984, 1985a,b, Shulman and Ogden 1987, Cowen and Castro 1994, Robertson 1988a,b, 1990, Wellington 1992; but see Victor 1986, Booth and Beretta 1994, Tolimieri 1995).

In this report, we examine the recruitment patterns of 14 species of Caribbean coral-reef fishes at 10 fore-reef sites on 3 islands over 4 years (Fig. 2.1, Table 2.1). We are interested in the patterns of recruitment at both the assemblage and the species level. Specifically, we ask: (1) How variable is recruitment and from where does the variation come (years, islands, sites within islands)? (2) Are spatial patterns consistent through time even if the absolute numbers of recruits are not? (3) Are there spatial correlations in recruitment among fish species? (4) What role do substratum characteristics play in determining the magnitude of recruitment? and (5) Do some sites always receive similar assemblage-level recruitment to each other within years? Question 5 is a slightly different

species. Individual sites might receive completely different levels of recruitment of individual species in when comparing one year to the next. However, the relative abundance and composition of fishes recruiting to two sites may always be similar within years regardless of variation between years.

Materials and Methods

Study sites

To examine spatial and temporal variation in recruitment, we quantified the abundance of juvenile fishes over four years (1991-1994) at ten sites in the waters around three islands in the US and British Virgin Islands. Sites were several hundred meters to 50+ km apart (Fig. 2.1). We sampled recruitment during the following periods: 1991: 9 July to 26 July; 1992: 18 July to 1 August; 1993: 11 July to 31 July; and 1994: July 16 to August 2. Four sites, Tague Bay East, Central, and West, and Cane Bay (TBE, TBC, TBW, and CB, respectively), were located on the northern coast of St. Croix, USVI. Three sites, Tektite, Yawzi Point, Fish Bay (TK, YP, and FB), were located on the south coast of St. John, U.S.V.I.. The final three sites, Eustacia Reef, Mosquito Island, Mountain Point (ER, MI, MP), were located in the waters around Virgin Gorda, BVI. (Fig. 2.1). In 1991, we censused recruitment at all of the sites except MP. Although we report the 1991 data, we excluded them from most analyses due to problems caused by the missing cell at MP, and because they were censused slightly earlier in July than were the other sites.

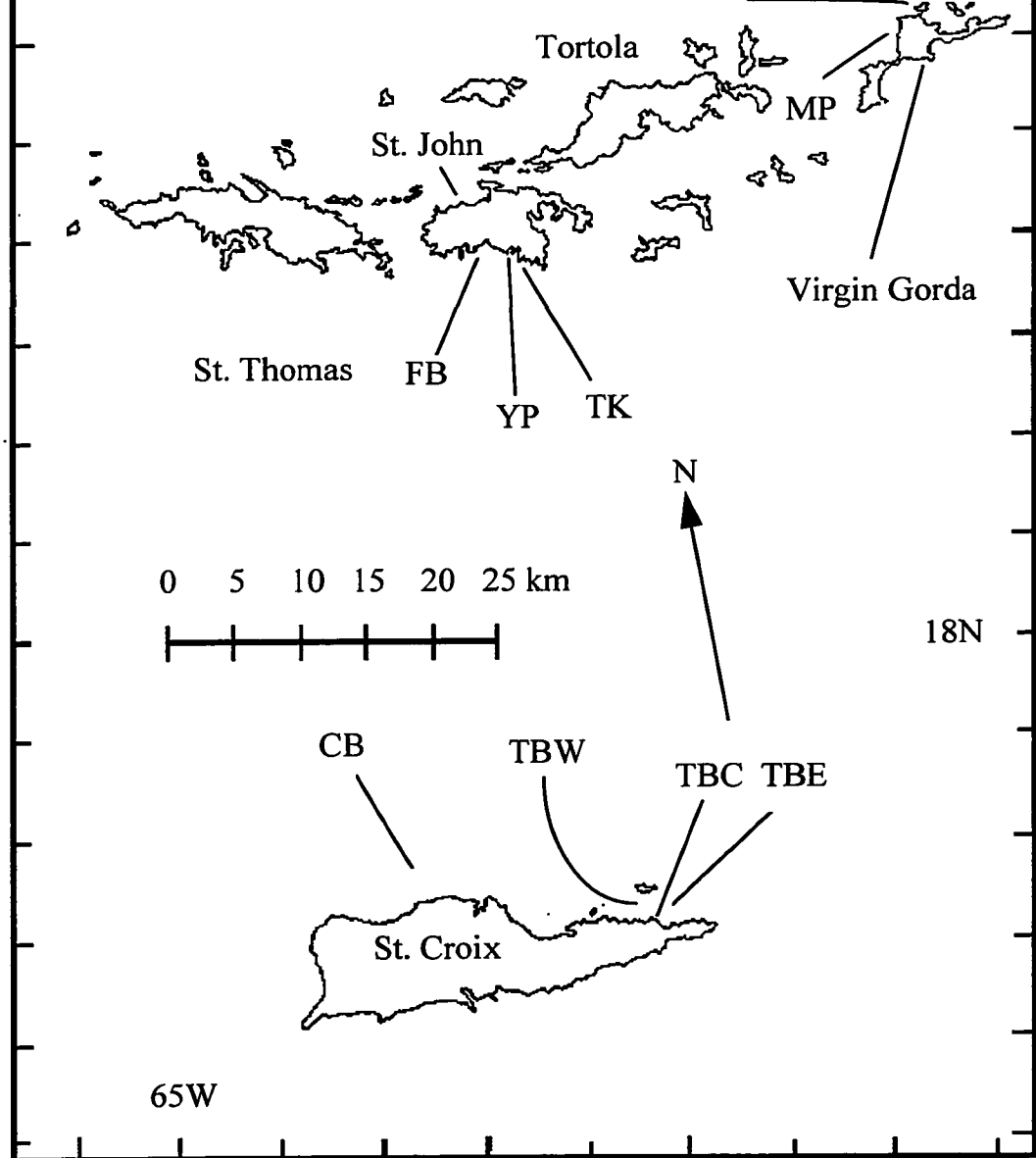


Figure 2.1. Locations of the study sites. TBE, TBC, TBW are Tague Bay east, central and west. CB = Cane Bay; TK = Tektite; YP = Yawzi Point; FB = Fish Bay; ER = Eustacia Reef; MI = Mosquito Island; MP = Mountain point.

Sites were chosen based primarily on accessibility and general habitat characteristics (we did not compare lagoon or back reef sites to more exposed sites), but they differed to some extent in slope, protection, and in the degree of scleractinian coral cover. The TBE,

Tague Bay barrier reef. Reef structure was primarily provided by dead elkhorn coral, *Acropora palmata* and both live and dead club finger coral, *Porites porites*. Heads of *Montastrea annularis* and other boulder corals were scattered throughout these sites as well. The reef base was from 8-15 m deep, but all sampling was conducted at approximately 10 m depth. Cane bay, a fringing reef with spur and groove structure, was located on the northwest end of the island. The reef began at approximately 8 m and at the study site continued to approximately 13 m, where an almost vertical wall descended to over 1000 m. At CB the cover of *P. porites* and *A. palmata* rubble was lower and dead boulder coral and coralline pavement made up a greater portion of the substratum than at the Tague Bay sites.

At the St. John sites TK and YP, most of the structure was provided by underlying basaltic boulders, which were encrusted by sponges, corals and gorgonians. The slope of the reef at these two sites was steeper than the TB sites or the area sampled at CB. TK and YP also differed from the other St. John site, FB, which was a more exposed fringing reef with spur and groove development. The base of all three sites was at approximately 10 to 15 m.

Like the three TB sites around St. Croix, the ER site on Virgin Gorda was also a fore-reef bank barrier reef, and the substratum was comprised primarily of dead *Acropora palmata*. The MI site was unlike most other sites in that it had high cover of soft corals and sea fans. At the MP site, *M. annularis* was more common than at other sites. This site also appeared to be somewhat more protected than other sites.

We quantified recruitment as the density of newly settled fish present along 30 x 1 m band transects in late July and early August (see sampling dates above). We followed the methods previously used on Australian reefs (Sale et al. 1984b, Eckert 1984, Fowler et al. 1992). Briefly, we haphazardly placed transects parallel to the shore line or reef-face at 6-10 m depth. A diver swam out a 30 m transect tape parallel with the reef slope. A second diver then waited five minutes before following along the transect and counting all recruits within a one meter strip. The width of the transect strip was delineated by a t-shaped bar one meter in width carried by the diver. Eight transects were done at each site in 1991. We increased the number of transects per site to 16 in the following years (1992-94). We focused on species that were not excessively cryptic and did not occur in schools too large to allow accurate counting. Post-dive briefings ensured uniform taxonomy, and we subsequently grouped two sets of 'difficult' species. Species included in the statistical analyses are noted in Table 2.1. The group *Scarus* spp. includes *S. iserti*, *S. guacamaia*, and *S. taeneopterus*. The juveniles of these species were difficult to distinguish. Likewise, we grouped several *Stegastes* species-*S. leucostictus*, *S. variabilis*, and *S. diencaeus*- because of difficulty in identifying them correctly. Based on the habitat we were sampling, the fish recorded in this category were probably all *S. variabilis* (Wellington 1992). For simplicity in presentation, these two groupings will be referred to as 'species', although we recognize that they are not monospecific groups.

Along these transects, we also quantified the microhabitat characteristics of each site. After the second diver counted the fish, the first diver swam along the same transect

every 25 cm along the transect. We recorded 13 different substrata, which we later reduced to two principal components (see below). 'Matrix' consisted of dead, eroded coral rubble and rock. The groupings 'Acropora rubble' and 'Porites rubble' included dead, usually broken corals, which still retained most of the structure of the living forms, *A. palmata* and *P. porites*. 'Porites' referred the living form of *P. porites*. Likewise 'Montastrea' included the living form of *M. annularis*, a large boulder-building coral. 'Pavement' consisted of eroded coralline rock that provided few or no holes. 'Algae' referred to areas that had dense macroalgal stands, even when the underlying structure was coralline in origin. The grouping 'massive', comprised all other massive, boulder and brain corals such as *Diploria* spp., *Siderastrea* spp., and *Copophyllia* spp.. We also recorded the groups: 'sand', 'sponge', 'branched soft coral', 'sea fan', and 'fire coral' (*Millepora*).

Statistical analyses

We used a 3-factor nested multivariate analysis of variance (MANOVA) to determine whether assemblage-level recruitment varied among years, islands, and sites nested within islands. MANOVA is similar to ANOVA except that it considers multiple dependent variables (here groups of fish species, see below) in the same analysis. In our analysis, years, islands and sites are random factors and sites are nested within islands. We chose to analyze all factors as random factors because no *a priori* reason existed for choosing particular years, sites or islands. Where MANOVA results were significant, we

determine which species or groups of species contributed to the assemblage-level effect.

In order to examine the dependent variables with post-MANOVA univariate F-tests, two considerations must be met. First, to protect the overall α , the critical p-values for rejection of the null hypothesis for each ANOVA must be adjusted (i.e., Bonferonni's adjustment). Second, to properly estimate the correct experimental alpha and p-value for each F-test, dependent variables must be uncorrelated (Tabachnick and Fidell 1989).

Because preliminary data analysis indicated correlations among species, we generated four principal components, which explained variation among sites in terms of recruitment of the 14 species of fish. Principal components analysis reduces the number of dependent variables, by linearly combining the dependent variables that are correlated into a new variable, the principal component (PC). Component loadings indicate the degree of association between the original variables and the principal components. When loadings are > 0.30 , the original dependent variables are considered to contribute to the principal component (Tabachnick and Fidell 1989). We used these four principal components as the dependent variables in the MANOVA and univariate F-tests (the number of principal components was determined by examining eigen values and skree plots). The principal components analysis accomplished several things. Reduction of the number of dependent variables allowed us to make smaller reductions in our p-value for rejection of the null hypothesis in the univariate F-tests. Second, principal components analysis also yielded uncorrelated dependent variables, allowing us to correctly estimate our overall α . Third, the principal components generated by the analysis elucidated associations among the recruitment patterns of the 14 fish species, because species with correlated recruitment

on analysis of eigenvalues in a scree plot, and our ability to interpret the results (Tabachnick and Fidell 1989). Components were rotated with varimax rotation to increase interpretability (Tabachnick and Fidell 1989). The p-value for rejection of the null hypothesis in the univariate F-tests is: $p < 0.0125$. Prior to running the principal components analysis, data were inverse transformed to homogenize variance and normalize the data. Variances for only some of the species were homogenized sufficiently by this procedure (Cochran's test, $p_{\text{crit}} = 0.05$) (Zar 1984). As a result, variances of PC3 and PC4 were homogenized (Cochran's test, $p > 0.05$), but variances for PC1 and PC2 were not homogenized (Cochran's test, PC 1: $0.05 > p > 0.01$, PC 2: $p < 0.01$), so results should be interpreted cautiously.

To determine the extent of the added variance caused by each independent variable (year, island, site), we calculated variance components for each of the 14 species. Variance components indicate the importance of each factor in contributing to the overall variation in the dependent variable. For each species, we first partitioned the variance with ANOVA on un-transformed, raw recruitment data (not the principal components). Variance components were then calculated from these models. We followed this procedure to retain as much species specific information as possible. Variance components analysis indicated which factors were most important because it indicates how much of the variance in a dependent variable is due to each factor (years, islands, sites). To allow for comparisons among species, we also calculated the % of the explained variance (i.e. variance not included in the error term) that was attributable to each main effect and the interactions. This second set of calculations standardizes values

two species may differ in the amount of unexplained variance (error), but the proportion of the explained variance explained by each factor may be similar. This conclusion is not readily apparent unless the second calculation is made. Because we performed no hypothesis tests here, the results are not affected by multiple tests or correlations among species.

To examine the variation in spatial pattern of recruitment among sites, irrespective of the actual amount of recruitment, we ranked sites and performed a concordance analysis (Zar 1984). Species were analyzed separately. Concordance analysis determines whether the ranking of sites (within years) is more similar from year to year than would be expected by chance. Kendall's coefficient of concordance (W) is equivalent to Spearman's rank correlation coefficient (Zar 1984).

To examine the relationship between substratum characteristics and recruitment, we first performed two separate principal components analyses on the mean recruitment across years at each site for fishes and the mean substratum characteristics for each site. We used principal components analysis to generate uncorrelated dependent variables (fish) and to reduce the number of independent variables (substrata) to a number allowed by our level of replication (Tabachnick and Fidell 1989). We then used recruitment principal components and substratum principal components as variables in multiple regressions to determine whether substratum variables explained variation in recruitment. Therefore, each site contributes one datum to the regression per year. Each dependent variable (fish principal component) was analyzed separately.

assemblage-level recruitment relative to others from year to year. In the analysis, we used mean recruitment (not recruitment per transect) of each of the 14 species at each site in each year as the variables to measure similarity among sites (see Table 2.1 for the species included in the analysis). Therefore, each species contributes one datum per site per year. Similarity among sites was calculated as Euclidean distance, and sites were joined using Ward's technique, which joins centroids (Wilkinson et al. 1992). Data for each year were analyzed separately. We then conducted a similar analysis based on the mean values of the 13 microhabitat characteristics recorded at the ten sites. Data for each year were analyzed separately. Our goal was to see whether sites clustered the same way in terms of recruitment and microhabitat characteristics.

Comparison with Australian data

Although there are exceptions in both cases, work on Caribbean reefs (Smith and Tyler 1972, 1973, 1975; Ebersole 1980, 1985; Forrester 1995; Robertson 1995, 1996) has tended to stress equilibrilibril ideas (but see Victor 1983, 1986), while work from Australian reefs has stressed the stochastic or non-equilibrial nature of reef fish populations (Sale 1977; Doherty 1983; Doherty and Fowler 1994a,b; but see, for example work by Jones 1986, 1987a,b, 1988a; Forrester 1990). In addition, several studies have demonstrated differences between Atlantic and Pacific fauna in egg size, larval duration and in abundance of taxa (Thresher 1991; Thresher and Brothers 1989). We therefore thought it appropriate to compare recruitment variation in Caribbean reef fishes to data in

levels of recruitment variation were comparable between regions.

Sale et al. (1984b) examined recruitment to fore-reef sites on Australian reefs at a similar spatial scale to our study (a sampling area 70 km in extent). They present recruitment data for 18 species at seven fore-reef sites on the Great Barrier Reef (GBR). For nine of the 18 species, they presented the means in each of two years, while for the other nine species, they gave only a mean over two years because there was no significant interaction between sites and years. We calculated the coefficient of variation (CV) for each species in our data set and for each species presented in Sale et al. (1984b) to allow for comparisons between the data sets, and to determine whether recruitment at this spatial scale was more variable on Caribbean or Australian reefs. We made two sets of calculations on the Australian data and our current data. First, for the nine species in Sale et al. (1984b) where mean recruitment in each year was shown and for all the Caribbean species, we used the mean recruitment at a site per year to calculate a CV value for each species. Therefore, CV's calculated from Sale et al. (1984b) have an $n = 14$ (7 sites x 2 years), while the CV's calculated from our present study have $n = 39$ (10 sites x 4 years - MP in 1991). These CV calculations included both spatial and temporal variation among sites. Second, we also calculated the CV for each species based on the mean recruitment at each site averaged over the two or four year period. These calculations were made on all 18 species in Sale et al. (1984b) and again for all the species analyzed in our current study. In this second set of calculations, CV's for each species from Sale et al. (1984b) have $n = 7$ (7 sites), while the CV's from our present study have $n = 10$ (10 sites). These CV values included only spatial variation.

Table 2.1. Recruitment of 40 species of fish recorded during recruitment censuses from 1991-1994 at 10 sites on three islands. 30x1 m transects were used record recruit abundance. Censuses were done in late July- early August of each year (1991, n = 8; 1992-94, n = 16). * indicates species included in the MANOVA, multiple regressions, and cluster analysis.

SPECIES	<u>1991-1994</u>	<u>1992-1994</u>	<u>1991-1994</u>	<u>1992-1994</u>
<i>Stegastes partitus</i> *	950	742	<i>Chaetodon capistratus</i>	3
<i>S. planifrons</i> *	198	185	<i>C. sedentarius</i>	0
<i>Stegastes</i> spp.*	340	311		
<i>S. dorsopunicans</i>	27	23	<i>Acanthurus coeruleus</i> *	130
<i>Microspathodon chrysurus</i>	13	11	<i>A. bahianus</i> *	170
<i>Chromis cyanea</i> *	985	618	<i>Holacanthus tricolor</i>	7
<i>C. multilineata</i> *	177	101		
			<i>Ocyurus chrysurus</i>	3
<i>Thalassoma bifasciatum</i> *	3145	2491	<i>Synodus intermedius</i>	2
<i>Halichoeres bivittatus</i>	33	30	<i>Epinephelus fuvus</i>	1
<i>H. maculipinna</i> *	112	90	<i>E. guttatus</i>	1
<i>H. garnoti</i> *	810	777	<i>Aulostomus maculatus</i>	3
<i>H. poeyi</i>	7	6		
<i>H. radiatus</i>	8	8	<i>Serranus tigrinus</i>	1
<i>Bodianus rufus</i>	12	10	<i>S. tabacarius</i>	1
<i>Clepticus parrai</i> *	170	170	<i>Hypoplectrus</i> spp.	31
			<i>Equetus punctatus</i>	3
<i>Scarus</i> spp. *	1356	1188	<i>Gramma loreto</i>	38
<i>S. vetula</i>	57	57		
<i>Sparisoma viride</i> *	710	607	<i>Lactophrys bicaudalis</i>	2
<i>S. aurofrenatum</i> *	390	390	<i>Canthigaster rostrata</i>	14
<i>S. automarium</i>	5	5	<i>Cantherhines pullus</i>	2
<i>S. radians</i>	2	2		
<i>S. chrysopterum</i>	5	5		
			TOTAL RECRUITS:	9928
				8137

We recorded a total of 9928 recruits of 40 species from 1991 to 1994 (Table 2.1, Fig. 2.2). We recorded 8137 of these recruits during the 1992-1994 censuses, for which we had a balanced sampling design. The 14 most abundant species made up >95% of all individuals recorded.

Principal components analysis showed that *Chromis cyanea*, *C. multilineata*, and *Clepticus parrai* loaded on PC1 (Table 2.2). *Acanthurus coeruleus*, *A. bahianus* and *Halichoeres maculipinna* loaded on PC2. *H. garnoti*, *Sparisoma aurofrenatum*, and *Stegastes* spp. loaded on PC3. *S. planifrons*, *S. viride*, and *Scarus* spp. loaded on PC4. Two species, *Thalassoma bifasciatum* and *S. partitus* loaded ambiguously on more than one principal component, although the highest loadings were on PC1. The reader should note that the variance explained by the PC analysis was relatively low. However, the general results are consistent with those derived from the analysis of variance components (see below), which were derived from the raw data, suggesting that the PCA results are robust.

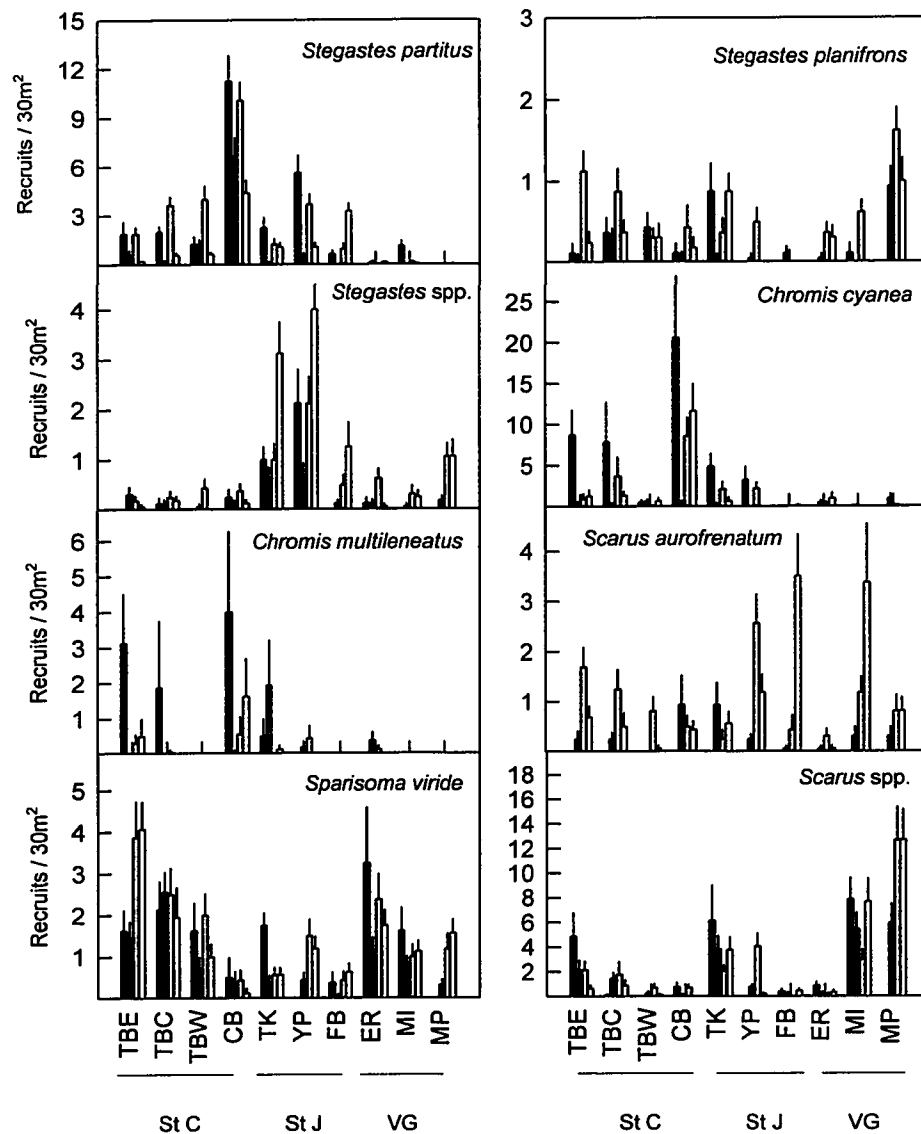


Figure 2.2a. Mean recruit abundance ($\pm 1SE$) along 30 x 1 m transects. Black bars indicate 1991, Dark grey 1992, light grey 1993, white 1994. Site locations are given on figure 2.1

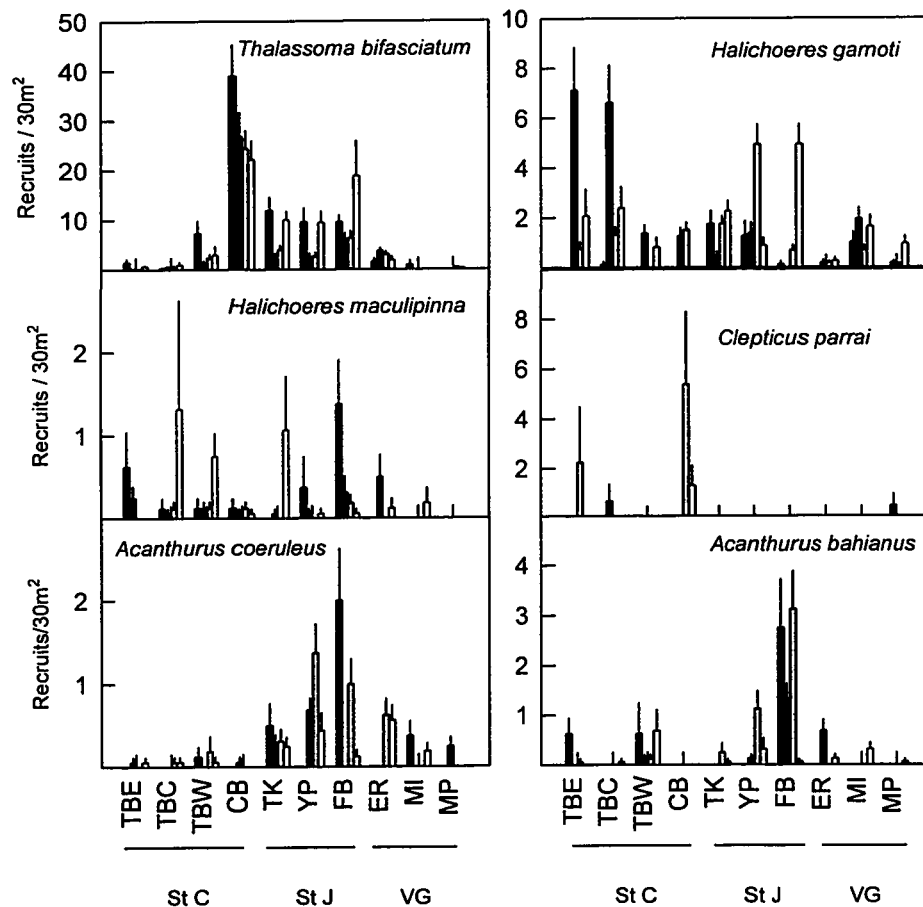


Figure 2.2b. Mean abundance of recruits along 30 X 1 meter transects at 10 sites over 4 years. Black bars indicate 1991; Dark grey 1992; Light grey 1993; white 1994. Site locations are given on Fig. 2.1. Sites connected with lines were on the same island.

MANOVA indicated that assemblage-level recruitment for 1992-94 varied among islands and among sites within islands (Table 2.3). However, there were also significant year*island and site*year interactions, indicating that recruitment intensity differed among sites in a different way each year. Assemblage-level recruitment did not differ

recruits arriving at these sites.

Table 2.2. Rotated component loadings for principal component analysis (correlation matrix) describing variation among sites in terms of fish recruitment. PC's were rotated with varimax rotation. Data were inverse transformed prior to analysis ($1/[x+1]$). Loadings greater than 0.30 or less than -0.30 are indicated in bold.

Species	PC1	PC2	PC3	PC4
<i>Chromis cyanea</i>	0.806	0.038	0.068	0.092
<i>Ch. multilineata</i>	0.632	-0.077	-0.217	0.139
<i>Clepticus parrai</i>	0.521	0.129	-0.050	0.044
<i>Stegastes partitus</i>	0.547	0.000	0.384	-0.346
<i>Thalassoma bifasciatum</i>	0.449	-0.442	0.127	-0.364
<i>Acanthurus coeruleus</i>	-0.064	-0.705	0.173	0.107
<i>A. bahianus</i>	-0.143	-0.693	-0.036	-0.150
<i>Halichoeres maculipinna</i>	0.052	-0.429	-0.227	-0.024
<i>H. garnoti</i>	-0.030	0.097	0.667	0.080
<i>Sparisoma aurofrenatum</i>	-0.115	0.101	0.634	0.151
<i>Stegastes spp.</i>	0.107	-0.269	0.546	0.079
<i>St. planifrons</i>	0.125	0.003	-0.009	0.673
<i>Scarus spp.</i>	-0.063	0.100	0.223	0.653
<i>Sp. viride</i>	0.060	-0.002	0.105	0.580
% of variance explained by each component	13.6	10.5	10.9	11.2

Variance in PC1 (*Chromis cyanea*, *C. multilineata*, *Clepticus parrai*) and PC2 (*Acanthurus coeruleus*, *A. bahianus*, *Halichoeres maculipinna*) differed among islands (Table 2.4, Table 2.5). Neither group showed an interaction between years and islands, suggesting that recruitment varied among islands in a consistent way from one year to the

Croix particularly to CB (Fig. 2.2ab). Both *Acanthurus* species showed highest recruitment to YP on St. John (Fig. 2.2b). PC3 (*H. garnoti*, *Sparisoma aurofrenatum* and *Stegastes spp.*) showed a significant interaction between years and islands indicating that the intensity of recruitment changed in a different manner at each island from year to year. PC1 (*C. cyanea*, *C. multilineata*, *C. parrai*) and PC4 (*Stegastes planifrons*, *Sparisoma viride*, *Scarus spp.*) differed among sites within islands. However, there were significant interactions between years and sites within islands for all principal components, indicating that recruitment intensity changed in different ways at each site (within islands) from year to year.

Table 2.3. Results of MANOVA on fish recruitment to 10 sites on three islands for three years (1992-1994).

Source	df	Pillai trace	F	p
Year	8, 2	1.073	0.579	0.763
Island	8, 46	1.057	6.443	<0.001
Year*Island	16, 56	1.637	2.425	0.008
Site(Island)	28, 56	2.628	3.831	<0.001
Year*Site(island)	56, 1800	0.393	3.507	<0.001

For five species, *Stegastes partitus*, *S. planifrons*, *Thalassoma bifasciatum*, *Sparisoma viride*, and *Scarus spp.*, most of the variation was among sites within islands

the variation was due to the interaction between years and sites within islands. Explained variance was more evenly distributed among sites and year*sites for *Acanthurus coeruleus*, *A. bahianus*, *Chromis cyanea*, *C. multilineata*, *Clepticus parrai*, and *Stegastes* spp.. For *H. maculipinna*, the current model explained very little of the variation in recruitment (98% in the error term).

The results of concordance analysis agree well with those from analyzing added variance components (Table 2.4, Fig. 2.2); rankings of sites were consistent from year to year for species in which the majority of the added variance was due to variation among sites within islands. These species were: *Stegastes planifrons*, *S. partitus*, *Stegastes* spp., *Thalassoma bifasciatum*, *Sparisoma viride*, and *Scarus* spp.. For roughly half (8/14) of the species, however, the rankings of sites based on the intensity of recruitment varied from year to year.

MANOVA showed that substratum characteristics differed among sites (Pillai trace = 12.301, $F = 55.536$, $df = 117, 4754$, $p < 0.001$, years were pooled, Fig. 2.3). Table 2.6 shows the rotated component loadings for both mean fish recruitment and mean substratum characters, as well as the r^2 and p-values for each multiple regression between fish principal components and the two substratum principal components. There were weak relationships (17 - 22% of the variation explained) between substratum and three of the four fish principal components. These results do not necessarily show a causal relationship between substratum characteristics and recruitment, however, because similar process may affect both recruitment of fish and the distribution of coral and other

predictable from substratum characteristics.

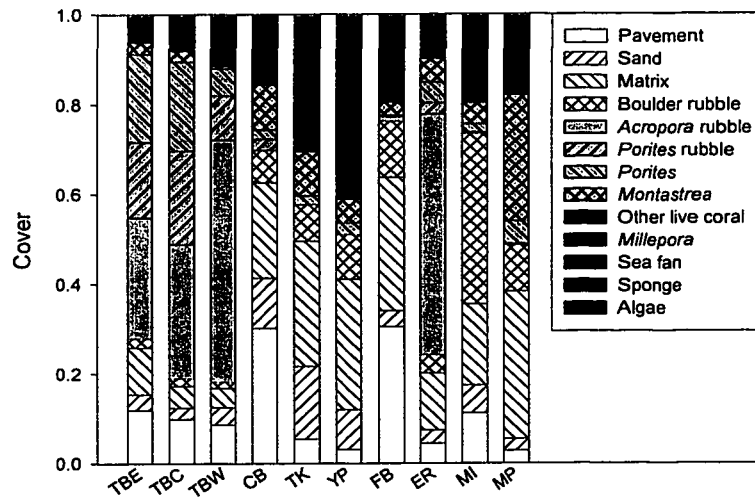


Figure 2.3. Cover of 13 substratum types at the 10 study sites. Data are averaged over 4 years.

Similarity among sites in recruitment and microhabitat characteristics

Figure 2.4 shows the results of cluster analysis on similarity of assemblage-level recruitment among the 10 sites. The most obvious trend is the dissimilarity of CB to all other sites in three of four years. In 1994 CB was not as dissimilar to other sites as in the previous three years, but it was more similar to sites on St. John than to sites on St. Croix. Also, some sites were generally similar to each other. TBE and TBC received

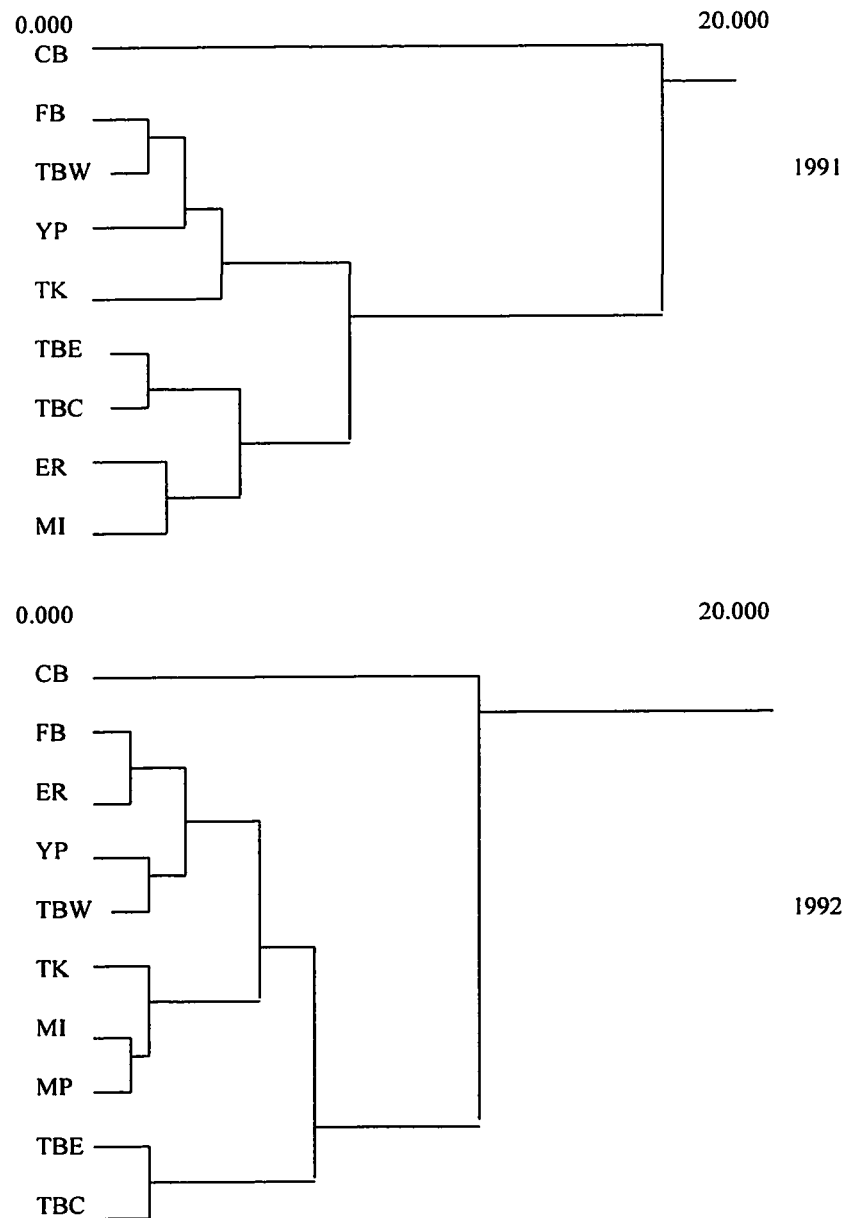


Figure 2.4ab. Results of cluster analysis linking sites based on fish recruitment for (a) 1991 and (b) 1992

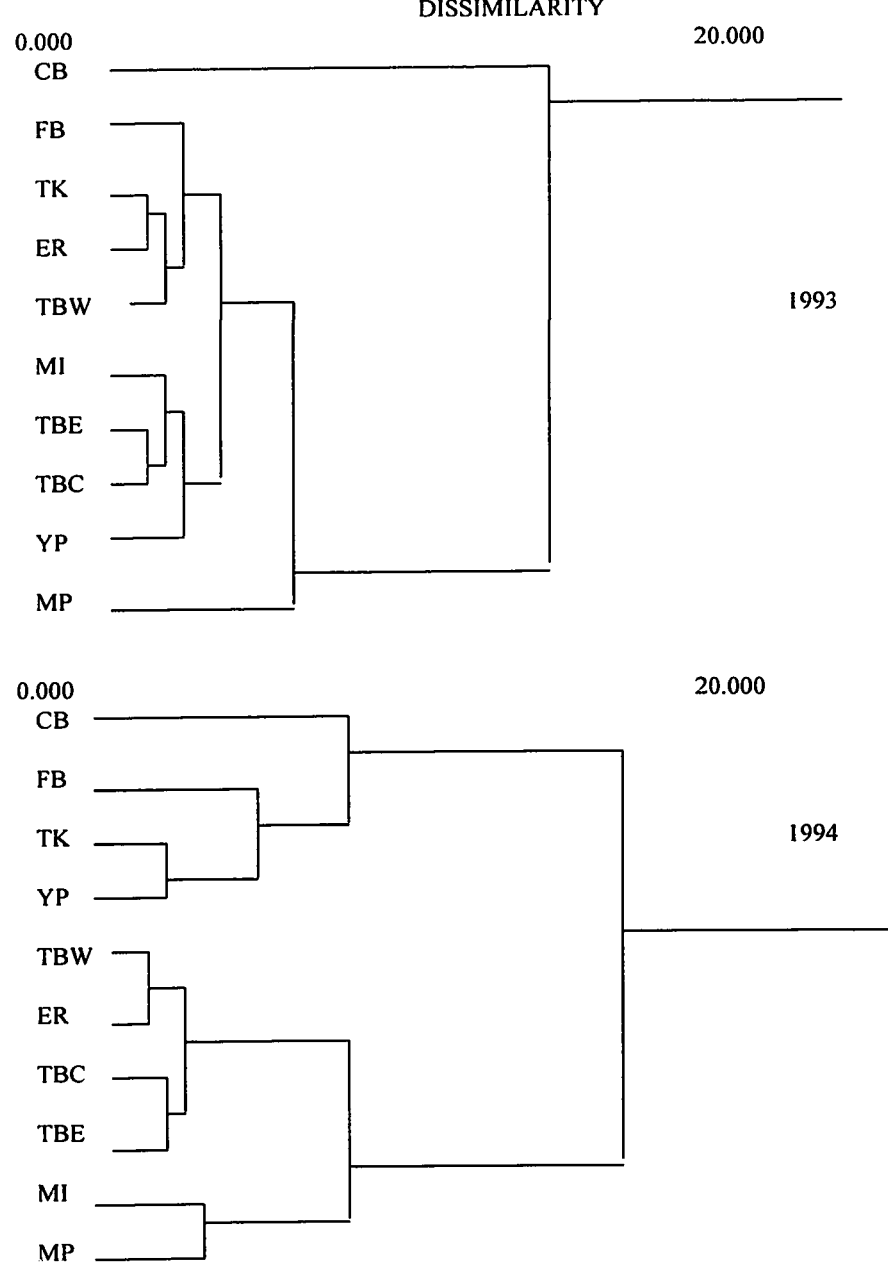


Figure 2.4cd. Results of cluster analysis linking sites based on fish recruitment for (c) 1993 and (d) 1994

Likewise, TBW was most similar to ER in 1994. In 1992 and 1993 when TBW and ER were not joined at the first connection, they were joined at the next. In 1991, however,

even more variable.

Pairing of sites based on microhabitat characteristics was stable across years (Fig. 2.5). Three pairs of sites were most similar to each other in all years: TBE-TBC; TBW-ER; and TK-YP. The four *Acropora palmata*-dominated bank fore-reef sites (TBE, TBC, TBW, and ER) separated from the other six sites in three out of four years (Fig. 2.3, Fig. 2.5). One pair of sites, CB-FB, was most similar to each other in three out of four years. In both cases, the odd year came in 1991 when only eight transects were done at each site. MI and MP were unlike each other in two of three years (MP was not censused in 1991).

Relationships of sites based on microhabitat characteristics (Fig. 2.5) paralleled the clustering based on recruitment (Fig. 2.4) in some cases, but showed differences as well. TBE and TBC clustered together as did TBW and ER. However, CB did not separate from the other sites in microhabitat characteristics as it did when the sites were clustered using recruitment values.

Comparisons with Australian data

Table 2.7 shows the coefficients of variation in recruitment for data from Sale et al. (1984a). Spatio-temporal variation (the first set of CV's) was higher in the Caribbean ($n = 14$, mean CV = 1.682, SE = 0.678) than on the GBR ($n = 9$, mean CV = 1.035, SD =

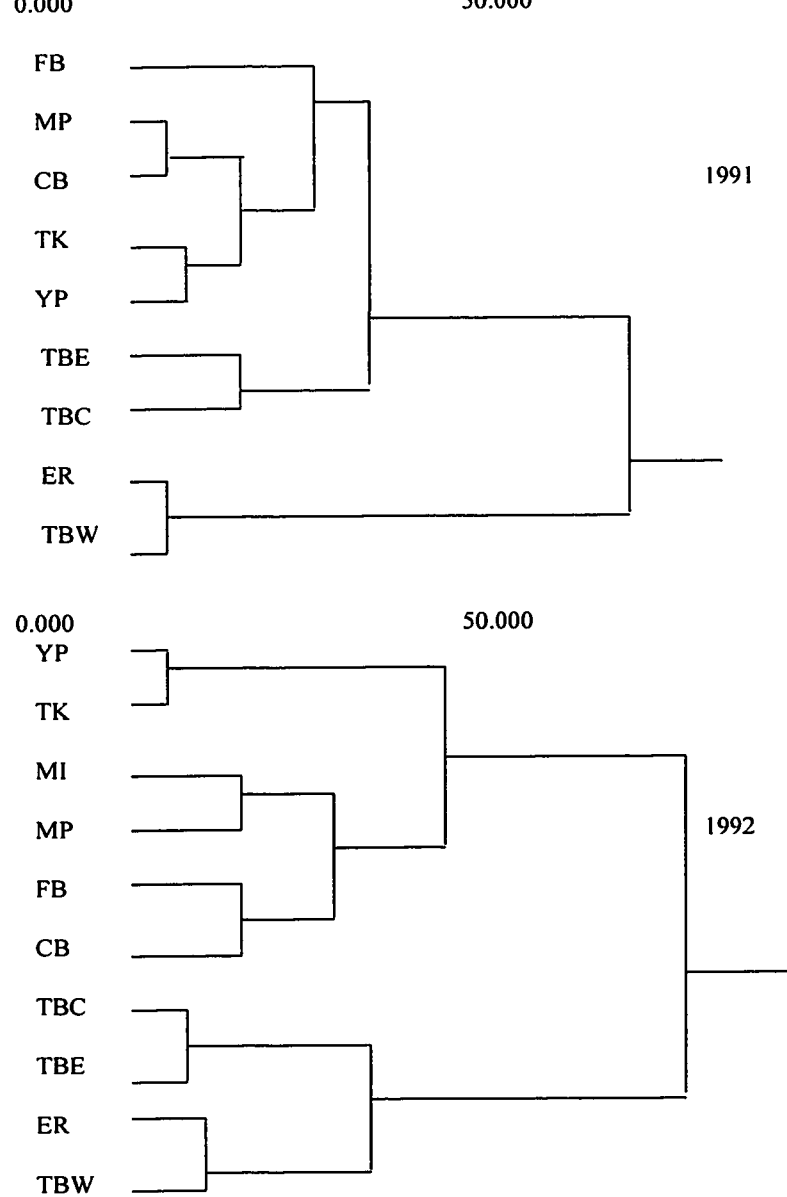


Figure 2.5ab. Results of cluster analysis linking sites based on microhabitat for (a) 1991 and (b) 1992

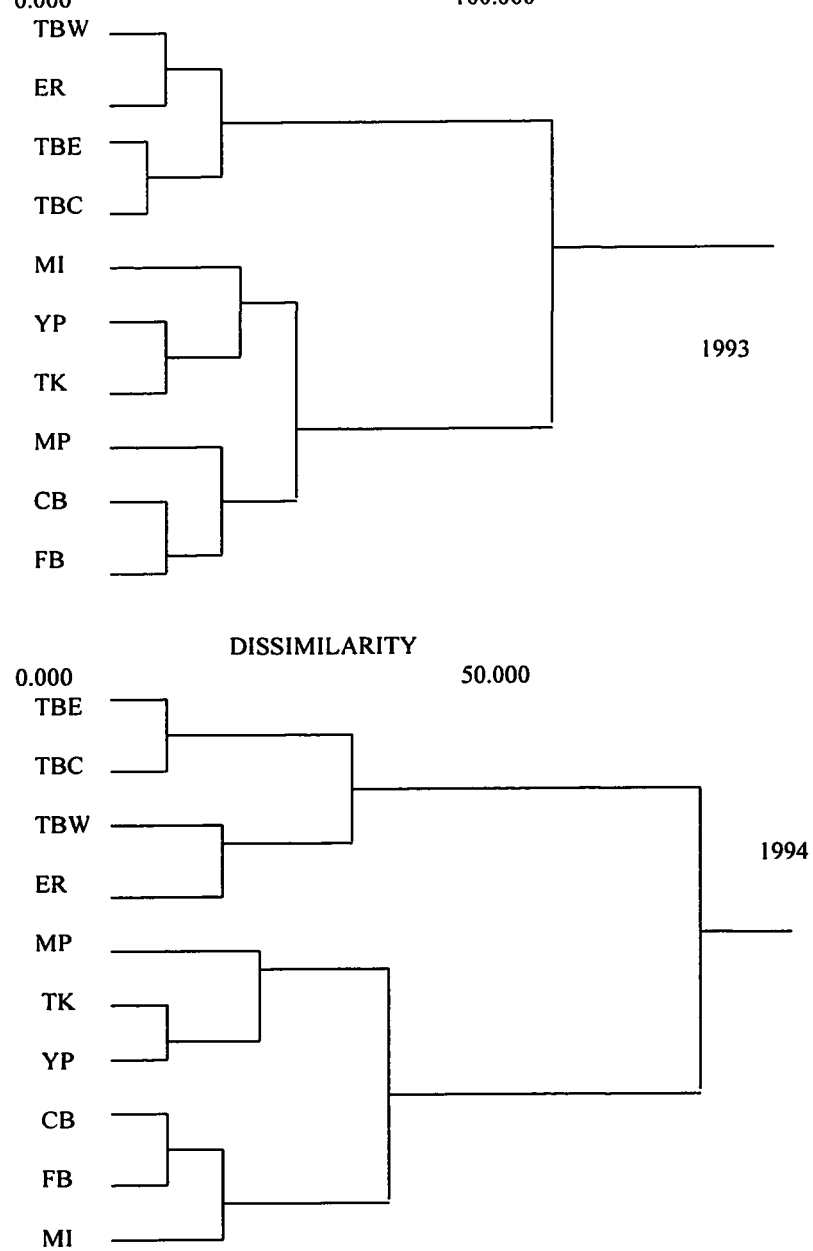


Figure 2.5cd. Results of cluster analysis linking sites based on microhabitat for (c) 1993 and (d) 1994

= 0.01). Likewise, when only spatial variation was considered, variation in recruitment of Caribbean reef fish ($n = 14$, mean CV = 1.167, SD = 0.428) was significantly higher than variation in recruitment of GBR reef fish ($n = 18$, mean CV = 0.863, SD = 0.298) at this spatial scale (separate variance t-test, $t = 2.261$, $df = 22.2$, $p = 0.034$).

Discussion

We found considerable spatial and temporal variation in recruitment, as well as several consistent spatial patterns at the assemblage and species level. Our results also indicated differences in the ways in which recruitment varied among species. The detection of large differences in the replenishment of local populations of reef fish is not a new phenomenon, but observations of consistent spatial patterns of recruitment have not been stressed by previous workers (Sale et al. 1984b, Victor 1986, Fowler et al. 1992, Milicich et al. 1992, Planes et al. 1993, Doherty and Fowler 1994a,b, Williams et al. 1994).

Our censuses recorded recruitment at each site at similar dates each year (1991 data were collected somewhat earlier, but were not included in most statistical analyses). This is a measure of recruitment success during that time of year. Direct comparisons across years are possible only when recruitment surveys are done at similar times. Williams et al. (1994) recently showed for GBR species that end-of-season surveys were as effective in estimating recruitment as a series of several surveys throughout the settlement season. Likewise, Levin (1996) found good correlations between settlement

Table 2.4. Results of Univariate F-test on the principal components used in MANOVA, as well as the added variance components and concordance analysis each species. The table shows the p-value for the F-test for each PC, and the % of the added variance due to each factor for each species. For variance components, numbers indicate the % of added variance to due each factor and unexplained added variance (error). Univariate F-tests were not conducted for the year main effect because MANOVA did not detect significant variation. nt = not tested. Years (Y) and islands (I) are random factors. Sites (S) are random and nested within islands. W = Kendall's coefficient. The null hypothesis is rejected at $p < 0.0125$ for the univariate F-tests.

PC/Species	Y	I	Y*I	S(I)	Y*S(I)	Error	W	P
PC1								
<i>Chromis cyanea</i>	p=nt %=0.1	0.012	0.078	<0.001	0.007	72.3	0.49	0.15
<i>C. multilineata</i>	0	0	0.2	13.2	12.8	94.7	0.44	0.21
<i>Clepticus parrai</i>	0	0.4	0.3	1.4	3.2	93.4	0.16	0.89
				1.7	4.2			
PC2								
<i>Acanthurus coeruleus</i>	p=nt	<0.001	0.297	0.118	<0.001	78.9	0.44	0.21
<i>A. bahianus</i>	%=0.4	4.3	2.3	6.2	7.9	66.6	0.52	0.13
<i>Halichoeres maculipinna</i>	0	2.7	5.0	9.7	16.0	97.7	0.49	0.15
	0.5	0	0	0	1.8			
PC3								
<i>Sparisoma aurofrenatum</i>	p=nt	0.016	0.005	0.068	<0.001	76.5	0.41	0.26
<i>Halichoeres garnoti</i>	%=1.5	0	0	0	22.0	65.4	0.47	0.18
<i>Stegastes</i> spp.	0	1.0	5.4	3.2	25.0	66.3	0.70	0.03
	0.7	9.0	8.6	11.4	4.0			
PC4								
<i>Stegastes planifrons</i>	p=nt	0.013	0.558	<0.001	0.004	75.4	0.67	0.03
<i>Scarus</i> spp.	%=2.3	0.7	0	17.6	4.0	59.9	0.82	0.008
<i>Sparisoma viride</i>	0	5.7	0.2	27.6	6.6	72.9	0.86	0.006
	1.4	2.2	0	18.0	5.5			
OTHER								
<i>Thalassoma bifasciatum</i>	%=0	1.3	2.0	46.0	0	50.7	0.95	0.002
<i>Stegastes partitus</i>	0.8	6.5	4.1	40.0	7.5	41.1	0.72	0.02

= 0.01). Likewise, when only spatial variation was considered, variation in recruitment of Caribbean reef fish ($n = 14$, mean CV = 1.167, SD = 0.428) was significantly higher than variation in recruitment of GBR reef fish ($n = 18$, mean CV = 0.863, SD = 0.298) at this spatial scale (separate variance t-test, $t = 2.261$, $df = 22.2$, $p = 0.034$).

Discussion

We found considerable spatial and temporal variation in recruitment, as well as several consistent spatial patterns at the assemblage and species level. Our results also indicated differences in the ways in which recruitment varied among species. The detection of large differences in the replenishment of local populations of reef fish is not a new phenomenon, but observations of consistent spatial patterns of recruitment have not been stressed by previous workers (Sale et al. 1984b, Victor 1986, Fowler et al. 1992, Milicich et al. 1992, Planes et al. 1993, Doherty and Fowler 1994a,b, Williams et al. 1994).

Our censuses recorded recruitment at each site at similar dates each year (1991 data were collected somewhat earlier, but were not included in most statistical analyses). This is a measure of recruitment success during that time of year. Direct comparisons across years are possible only when recruitment surveys are done at similar times. Williams et al. (1994) recently showed for GBR species that end-of-season surveys were as effective in estimating recruitment as a series of several surveys throughout the settlement season. Likewise, Levin (1996) found good correlations between settlement

Table 2.5. Results of variance components analysis. Numbers indicate the % of explained variance (i.e. not including variance in the error term) due to each factor to allow for comparisons among species.

PC/Species	Y	I	Y*I	S(I)	Y*S(I)
<i>Chromis cyanea</i>	0.4	5.0	0.7	47.7	46.2
<i>C. multilineata</i>	0	0	13.2	26.4	60.4
<i>Clepticus parrai</i>	0	6.0	5.0	25.8	63.6
<i>Acanthurus coeruleus</i>	1.9	20.4	11.0	29.4	37.4
<i>A. bahianus</i>	0	8.0	14.9	29.0	47.9
<i>Halichoeres maculipinna</i>	18.5	0	0	81.4	0
<i>Sparisoma aurofrenatum</i>	6.4	0	0	0	93.2
<i>H. garnoti</i>	0	2.9	15.6	9.2	72.5
<i>Stegastes spp.</i>	2.0	26.7	25.5	33.8	11.8
<i>Stegastes planifrons</i>	9.3	2.8	0	71.5	16.2
<i>Scarus spp.</i>	0	14.2	0.4	68.8	16.5
<i>S. viride</i>	5.0	8.0	0	66.4	20.3
<i>Thalassoma bifasciatum</i>	0	2.6	4.0	93.4	
<i>Stegastes partitus</i>	1.3	11.0	7.0	67.9	12.7

correlations with larval supply. However, our results are not intended to estimate settlement and should not be interpreted as such.

We detected two general types of recruitment pattern. All species groups showed significant interactions between site and year suggesting that recruitment intensity did not change in the same manner at all sites from year to year. This result implies variable and potentially stochastic recruitment because the spatial pattern of recruitment varied from year to year. However, results of the analysis of added variance components and concordance analysis indicate that this conclusion is not justified for six of the 14 species. For five species, most of the added variance was due to variation among sites and not the interaction between sites and years, and a total of six species showed consistent ranking of sites through time. The ranking of sites remained significantly similar from year to year for the three *Stegastes* species, as well as *Sparisoma viride*, *Scarus* spp., and *Thalassoma bifasciatum*. This pattern of similar ranking from year to year is demonstrated most clearly by the bluehead wrasse, *T. bifasciatum*, which always had the highest recruitment at the CB site.

The second type of recruitment pattern was most clearly demonstrated by species like *Halichoeres garnoti* and *Sparisoma aurofrenatum*. These species did not have temporally consistent spatial patterns of recruitment (ranking of sites from year to year), and most of the added variance was due to the interaction between sites and years. For example, *H. garnoti* had a strong pulse of recruitment each year, but this pulse was at a

Table 2.6. Rotated component loadings for principal component analysis describing variation among sites in terms of mean abundance of recruits at each site and mean substratum characteristics at each sites. PCA's for fish and substrata were done separately. R^2 and p-values for each fish PC are from multiple regressions between that PC and the two PC's derived from the substratum analysis. PC's were rotated with varimax rotation. Both PCA's and the regressions include data from 1991-1994 (n = 39).

Species	PC1	PC2	PC3	PC4	Substrata	PC1	PC2
<i>Stegastes partitus</i>	-0.912	0.081	0.104	0.137	massive coral rubble	0.854	-0.004
<i>Thalassoma bifasciatum</i>	-0.885	-0.138	0.092	0.188	sea fan	0.853	0.11
<i>Chromis cyanea</i>	-0.862	-0.108	-0.337	-0.025	<i>Porites</i> rubble	-0.812	0.21
<i>Ch. multilineata</i>	-0.671	0.054	-0.457	-0.064	<i>Acropora</i> rubble	-0.729	0.22
<i>Clepticus parrai</i>	-0.444	0.284	0.143	0.069	branched soft coral	0.726	0.31
<i>Acanthurus bahianus</i>	0.150	-0.799	-0.091	0.219	<i>Porites porites</i>	-0.690	0.33
<i>A. coeruleus</i>	0.150	-0.769	0.150	0.047	sponge	0.565	0.11
<i>Halichoeres maculipinna</i>	0.071	-0.569	-0.186	0.136	matrix	0.519	-0.11
<i>Sp. viride</i>	0.396	0.568	-0.078	0.019	<i>Montastraea annularis</i>	0.471	0.11
<i>Sparisoma aurofrenatum</i>	-0.004	0.067	0.734	0.144	sand	0.136	-0.71
<i>H. garnoti</i>	0.120	0.174	0.682	0.176	<i>Millepora</i>	0.075	0.63
<i>Stegastes spp.</i>	-0.121	-0.298	0.585	-0.324	pavement	0.004	-0.51
<i>Scarus spp.</i>	0.171	0.081	0.036	-0.873	algae	-0.005	-0.41
<i>St. planifrons</i>	0.080	0.261	0.069	-0.784			
% of variation explained by each component	23.4%	15.7	12.8	11.9		34.5	15.2
$r^2 =$	0.185	0.222	0.088	0.174			
p =	0.025	0.011	0.191	0.032			

1993 and FB in 1994.

Cluster analysis also indicated that some of the pattern of similarity in assemblage-level recruitment among sites was consistent through time (Fig 2.4a,b). Similarity in recruitment between TBE and TBC can be explained in part by their close proximity to one another. However, TBW was equally close to TBC as was TBC to TBE yet TBW received assemblage-level recruitment that was more similar to ER, which was on a different island. This pattern suggests that proximity was not the only factor determining similar patterns of recruitment. Conversely, CB was dissimilar to all sites in three out of four years. The pattern of similarity among the other sites was not consistent. Again, there is considerable variability, but also consistency in some cases.

Some associations among species are apparent. PC1 is comprised of planktivorous species (*Chromis cyanea*, *C. multilineata* and *Clepticus parrai*), and all these species showed their highest recruitment at CB. The two *Chromis* species showed high recruitment at this site relative to other sites in three of four years, as did *C. parrai* in two out of three years, (this species was not censused in 1991). *Thalassoma bifasciatum* and *Stegastes partitus* are partially planktivorous and always showed the higher recruitment to CB than to other sites as well, although they did not load cleanly on any one principal component. The CB reef is located just inshore of a steep drop-off, and hydrodynamic aspects of this location may result in higher planktonic food supply at this site. Diurnal planktivores are typically more abundant along reef edges that are adjacent to deeper water where their prey are more accessible (Hobson and Chess 1978;

Table 2.7. Coefficient of variation for recruitment of reef fishes from Sale et al. (1984) and the present study. The first CV for each species was calculated using the mean recruitment at each site for each year: for Caribbean species n=39, for GBR n=14. The second CV was calculated using only the mean recruitment at a site across all years: for Caribbean species n=10, for GBR n=7. n indicates the number of means used to calculate each CV. See text for further details.

Caribbean species	n=39	n=10	GBR species	n=14	n=7
<i>Stegastes partitis</i>	1.432	1.308	<i>Pomacentrus wardi</i>	0.725	0.677
<i>S. planifrons</i>	1.152	0.980	<i>Coris variegata</i>	0.761	0.755
<i>Stegastes</i> spp.	1.488	1.155	<i>Labryichthus unilineata</i>	1.302	1.295
<i>Chromis cyanea</i>	1.917	1.494	<i>Pseudolabrus guentheri</i>	1.947	1.793
<i>Ch. cyaneus</i>	2.213	1.294	<i>Stethojolis strigeveniter</i>	0.669	0.615
<i>Thalassoma bifasciatum</i>	1.451	1.432	<i>Scarus sordidus</i>	0.669	0.685
<i>Halichoeres maculipinna</i>	1.633	0.743	<i>Chelmon rostratus</i>	0.872	0.708
<i>H. garnoti</i>	1.291	0.677	<i>Canthigaster valentini</i>	1.283	0.811
<i>Clepticus parrai</i>	3.631	2.070	<i>Paraluteres prionurus</i>	1.086	0.756
<i>Scarus</i> spp.	1.351	1.277	<i>Amphiprion akindynos</i>		1.125
<i>Sparisoma aurofrenatum</i>	1.378	0.577	<i>Dischistodus melanotus</i>		0.889
<i>Sp. viride</i>	0.769	0.662	<i>Chysiptera rollandi</i>		0.802
<i>Acanthurus coeruleus</i>	1.700	1.079	<i>Pomacentrus amboinensis</i>		0.839
<i>A. bahianus</i>	2.143	1.665	<i>P. molluccensis</i>		0.743
			<i>Halichoeres melanurus</i>		0.726
			<i>Labroides dimidiatus</i>		0.733
			<i>Thalassoma lunare</i>		1.069
			<i>Ostracion cubicus</i>		0.519

planktivorous species to CB is due to food supply, larval supply, habitat choice or higher post-settlement survival. Although both surgeonfish species loaded on the same component (PC2), there is no clear taxonomic or trophic grouping of the other species. For example, there is no principal component that is comprised of all wrasses or all parrotfish or all benthic herbivores. However, PC3 and PC4 do divide the benthic herbivores with temporally consistent patterns of recruitment from those in which recruitment patterns varied from year to year.

Australian and Caribbean reefs

Comparison of the coefficients of variation for recruitment of Caribbean and Australian reef fishes suggests that spatio-temporal variation in annual recruitment success is higher for fishes in the Caribbean. The cause of this difference in the magnitude of variation is impossible to discern from our data, but differences between the GBR and the Caribbean in larval duration of the species or consistency of longshore currents may be important. Thresher and Brothers (1989) note that the larval duration of many Pacific damselfishes and other demersal spawners is shorter than their counterparts in the Caribbean. Within our own data, the pomacentrids, which have larval durations of approximately four weeks (Thresher and Brothers 1989) do have lower CV's than both acanthurid species, which have larval durations of up to three months (Brothers et al. 1983, for GBR species).

patterns. Additionally, of the species that did have consistent spatial patterns, not all recruited to the same site. *Thalassoma bifasciatum* and *Stegastes partitus* both showed highest recruitment at CB, yet *Sparisoma viride*, *Scarus spp.*, *Stegastes planifrons*, and *Stegastes spp.* recruited to other sites. However, this conclusion should not be drawn from our data. This expectation assumes that larvae act as passive particles and that all species are equal in the plankton in terms of abundance and motility. Sponaugle and Cowen (1996) found that although some sites around Barbados always received higher overall larval supply, the relative abundances of individual taxa were not the same at all sites. Additionally, Cowen (1985) suggested that the patterns displayed by individual species may be the result of the location of the spawning populations. He found that variability in recruitment of *Semicossyphus pulcher* along the California and Baja coast was related to upstream sources. Areas with no upstream source showed high levels of variability and recruitment was dependent upon anomalous events in the current flow. Areas with upstream sources showed more consistent recruitment from year to year. Similarly, bay scallops, which have a much shorter pelagic stage, appear to be recruitment limited when adult population density is low because larval supply is more directly correlated with local production (Peterson and Summerson 1992, Peterson et al. 1996).

Alternatively, species with strong microhabitat requirements may show spatially consistent patterns of recruitment, while species without strong requirements may demonstrate much more variable recruitment patterns. Habitat and microhabitat selection

1984a, Shulman 1984, Booth 1992, Tolimieri 1995, among others), and recent evidence shows that they can select between habitats as well (Wellington 1992, Doherty et al. 1996). Doherty and Fowler (1994b) suggested that species with strong microhabitat selection during settlement may show more spatial variation in recruitment, but these spatial patterns may be more consistent through time. This was the case for two species of pomacentrid that they studied on the Great Barrier Reef, Australia. *Pomacentrus moluccensis* selects live branched coral during settlement. This species showed 10-fold variation in recruitment but the pattern was consistent through time. Another species, *P. wardi* is less selective. It showed only five-fold variation in space, but the spatial pattern was not consistent through time. They suggested that variation in larval supply may have been slightly overridden by microhabitat selection.

The slight similarity between the cluster analysis of fish and the cluster analysis using substratum characteristics suggests that microhabitat features may play a minor role in determining recruitment. Likewise, the loading of all planktivores on the first principal component suggests that other habitat characteristics that we did not measure (e.g., current velocity, food supply) also may be important for these species. Doherty et al. (1996) provide evidence that larvae may be able to make general habitat choices while in the plankton, and work by other researchers suggests that larvae may not be entirely passive particles (Stobuzki and Bellwood 1994). The results of the regression analysis provide evidence that substratum characteristics may have a small effect at this spatial scale for some species because 17 - 22% of the variation in recruitment among sites was

components. It is, of course, impossible to discern from our data whether the effect is due to habitat or microhabitat choice during settlement or to post-settlement processes.

Conclusions

Variation in recruitment will have different consequences based on both the consistency of the spatial pattern and the life-span of the species. Species with temporally coherent spatial patterns of recruitment (ranking of sites) should maintain higher populations in some areas and lower populations in others, unless post-recruitment mortality is strongly compensatory or otherwise variable. At sites where recruitment is generally uniform from year to year (whether high or low), population size may also be more stable unless post-recruitment mortality is variable. In cases where spatial patterns are not consistent through time, the distribution and abundance of the meta-population is likely to be much more variable (Doherty 1983, Cowen 1985). In both cases, the life-span of the species is important because the local population dynamics of short-lived species will be more susceptible to variation in recruitment than would the population dynamics of long-lived species (Warner and Chesson 1985). Alternatively, long-lived species will be less susceptible to variation in recruitment because one good recruitment year can be 'stored' in the adult population for many years (Warner and Chesson 1985, Doherty and Fowler 1994a,b).

The importance of post-settlement processes may also be affected by variation in recruitment (e.g. Menge and Sutherland 1987). Jones (1990) provides a particularly

amboinensis to 8 m² patch reefs while at the same time monitoring recruitment to similarly sized unmanipulated patch reefs. Manipulated reefs indicated at what level of recruitment, density-dependent processes limited adult population size. He found that in some years recruitment to unmanipulated reefs was low (as indicated by the manipulative experiment), and adult population size was limited by recruitment. In other years, fifty percent of the unmanipulated reefs received high enough recruitment to make density-dependent processes important.

The situation may be somewhat more complicated than simple numerical variations in recruitment, however. Throughout this paper, we have used ‘high’ and ‘low’ to refer to recruitment in a relative sense, comparing one site to another or when comparing the intensity of recruitment among sites or across years. It should be noted that recruitment may also be high or low in relation to the availability of resources (Andrewartha and Birch 1954). Some reef fish populations appear to be recruitment limited (Victor 1983, 1986, Doherty and Fowler 1994a,b), and reef fish may be rare in relation to their resources. However, if consistent spatial patterns of recruitment are the result of interactions with habitat or microhabitat characteristics, recruits may be common in relation to their resources (possibly shelter). Recruit distributions might be determined by microhabitat choice during settlement but not limited thereafter. If this were the case, adult populations would be secondarily recruitment-limited by early post-settlement mortality mediated via substratum characteristics (*sensu* Victor 1986). Alternatively, the consistent spatial distributions that we saw may have been the result of current regimes,

understand the dynamics of reef fish populations and communities, it is important to determine what processes created the spatial patterns of recruitment that we observed.

RECRUITMENT AND ADULT ABUNDANCE IN THE STOPLIGHT PARROTFISH, *SPARISOMA VIRIDE*, AT THREE SPATIAL SCALES

Abstract

Most of the fishes on coral reefs produce pelagic larvae, and as a result, benthic, adult populations depend upon recruitment of individuals from the plankton. This study investigated the relationship between microhabitat characteristics and recruitment of *Sparisoma viride* (Scaridae), across three spatial scales. Analysis of 1.0 m² quadrats showed that within a habitat, *S. viride* recruits associated with club-finger coral, *Porites porites* (live + dead) more than would be expected at random. At a medium spatial scale, abundance of *S. viride* recruits differed among 12 sites in four habitats on the Tague Bay reef, St. Croix, U.S.V.I.. In general, recruitment was higher to the back reef than to the reef crest, reef slope and reef base. Recruitment was also higher to the reef slope than to the reef crest or reef base. Variation in mean abundance of recruits among sites and habitats was correlated with the percent cover of *Porites* in two years. At a larger spatial scale, the percent cover of *Porites* at 10 sites located on three islands (St. Croix, St. John, and Virgin Gorda) explained 66-81% of the variation in mean recruit abundance in three of four years. Contemporary adult abundance was correlated with mean recruitment at this spatial scale. These results suggest that the benthic environment plays a role in the replenishment of adult populations on local reef patches. Likewise, microhabitat

scales.

Introduction

The processes of dispersal and recruitment play an important role in the population dynamics of many marine invertebrates and fishes. These organisms live in patchy environments and produce pelagic larvae that disperse among patches (Thorson 1950; Sale 1980). A consequence of having a pelagic larval stage is that local reproduction and the replenishment of the adult population are uncoupled, and replenishment of a local patch is dependent upon the recruitment of larvae from the plankton. Recruitment success often has strong effects on the dynamics and abundance of local populations (Victor 1983, 1986; Gaines et al. 1985; Jones 1990; Raimondi 1990; Doherty and Fowler 1994a,b).

Coral reef fish are generally considered to exist in open populations (Doherty 1991; Sale 1991; but see Leis 1994). They have a two-part life cycle in which juveniles and adults are closely associated with the benthos, but all of the reproduction that occurs on a reef is exported from that patch via the production of pelagic eggs and/or larvae (Sale 1980 1991; Doherty and Williams 1988). These larvae develop in the plankton for 10 -100 days depending upon the species, after which they metamorphose into juveniles and settle to the benthic habitat. There is some evidence for self-recruitment (recruitment to the spawning population) in atoll lagoons or other similarly enclosed areas (e.g. Schmitt 1984; Leis 1994), but not in all cases (Danilowicz in press). The term settlement

is usually defined as the first sighting of juvenile fishes in the adult habitat.

Prior to settlement, oceanic currents, tidal cycles, stochastic storm events and variable survival of the larvae in the plankton can affect the availability of larvae to local patches (Victor 1983 1986; Leis 1991; Shenker et al. 1993; Thorrold et al. 1994a,b,c; Sponaugle and Cowen 1996). These are processes that occur away from the reef and over which factors within the local patch (e.g. competition or predation) have no influence. During settlement, habitat and microhabitat choice as well as interactions with resident fishes can determine settlement patterns (Sale et al. 1984a; Sweatman 1985, 1988; Booth 1992; Tolimieri 1995). Once juveniles are on the reef, competition, predation, interactions with other fishes, and responses to microhabitat characteristics become important (Sale 1971; Jones 1987a,b, 1988a; Clifton 1989, 1990, 1991; Hixon and Beets 1989, 1993; Forrester 1990, 1991; Booth 1995; Carr and Hixon 1995). Processes that influence recruitment during and after settlement operate at the level of the local reef patch. The strength of such factors determines to what extent the population dynamics of these species are determined by processes operating within the local patch.

There is abundant evidence that microhabitat characteristics are important in influencing the recruitment and the distribution of marine fishes at smaller spatial scales- i.e., within or among habitats, (Sale 1972b; Sale et al. 1984a; Jones 1988a; Levin 1991; Carr 1991; Booth 1992; Wellington 1992; Garcia-Rubies and Macpherson 1995; Tolimieri 1995; Caselle and Warner 1996). At larger spatial scales, variability in macroalgal structure often explains variability in the abundance of temperate reef fish

structural complexity generally support higher abundance and diversity of adult fishes (Luckhurst and Luckhurst 1978), but it is not known whether individual substrata influence the recruitment of particular species at these larger spatial scales (i.e. sites separated by many kilometers).

The stoplight parrotfish, *Sparisoma viride* (Teleostei: Scaridae), is a common herbivore on Caribbean coral reefs. It is a protogynous hermaphrodite (Reinboth 1968) and feeds on epiphytic algal turf, crustose coralline algae, and endolithic algae (Bruggemann et al. 1994a,b,c). Settlement to the reef occurs at approximately 10 mm standard length (SL) (pers. obs.). Fish mature at 170-270 mm SL and can attain lengths in excess of 500 mm. Sex change from female to male may occur at 150-250 mm SL (Koltes 1993). For the context of this study, I define recruits as juvenile fish in the range of 10-40 mm SL. These individuals are several days to several months old.

In this report, I examine recruitment variation in the stoplight parrotfish, *S. viride* across three spatial scales. My approach was (1) to determine what substrata *S. viride* used within a site, and (2) ask whether that substratum predicted variation in recruitment at larger spatial scales. Additionally, I determine (3) whether sites that generally receive higher recruitment than other sites also support higher adult populations.

Methods

In the context of this study, I define small scale as a scale of meters, in particular that of individual recruits. Medium spatial scale is measured in 100's of m² and applies

scale is measured in kilometers to 10's of kilometers and refers to sites separated by at least several kilometers. Sites encompassed areas approximately 1500-2000 m², and were separated by 100's of meters to several kilometers. Field work for the small and medium spatial scale aspects of this study was conducted on the Tague Bay reef, St. Croix, U.S.V.I. during the summers of 1994 and 1995 (Fig. 1). The Tague Bay reef was a bank barrier reef that encloses Tague Bay from the open ocean. Most of the reef's structure was provided by dead elkhorn coral, *Acropora palmata*, and club finger coral, *Porites porites*, with boulder corals such as *Montastrea annularis*, *Siderastrea* spp., *Diploria* spp. and *Copophylia* spp. scattered about the reef. The back reef was the sheltered, lagoon side of the reef and ranges from 2-5 m in depth. The lagoon floor consisted mostly of sand with some sea grass. The reef crest was 1.0 m to partially emergent at low tide and received high disturbance due to wave action. The reef slope was the ocean face of the reef in 3 - 10 m of water. The reef base was at a depth of 12-15 m. During the summer months, water appeared to flow westerly along the reef, although surface waters occasionally shifted direction (pers. obs.).

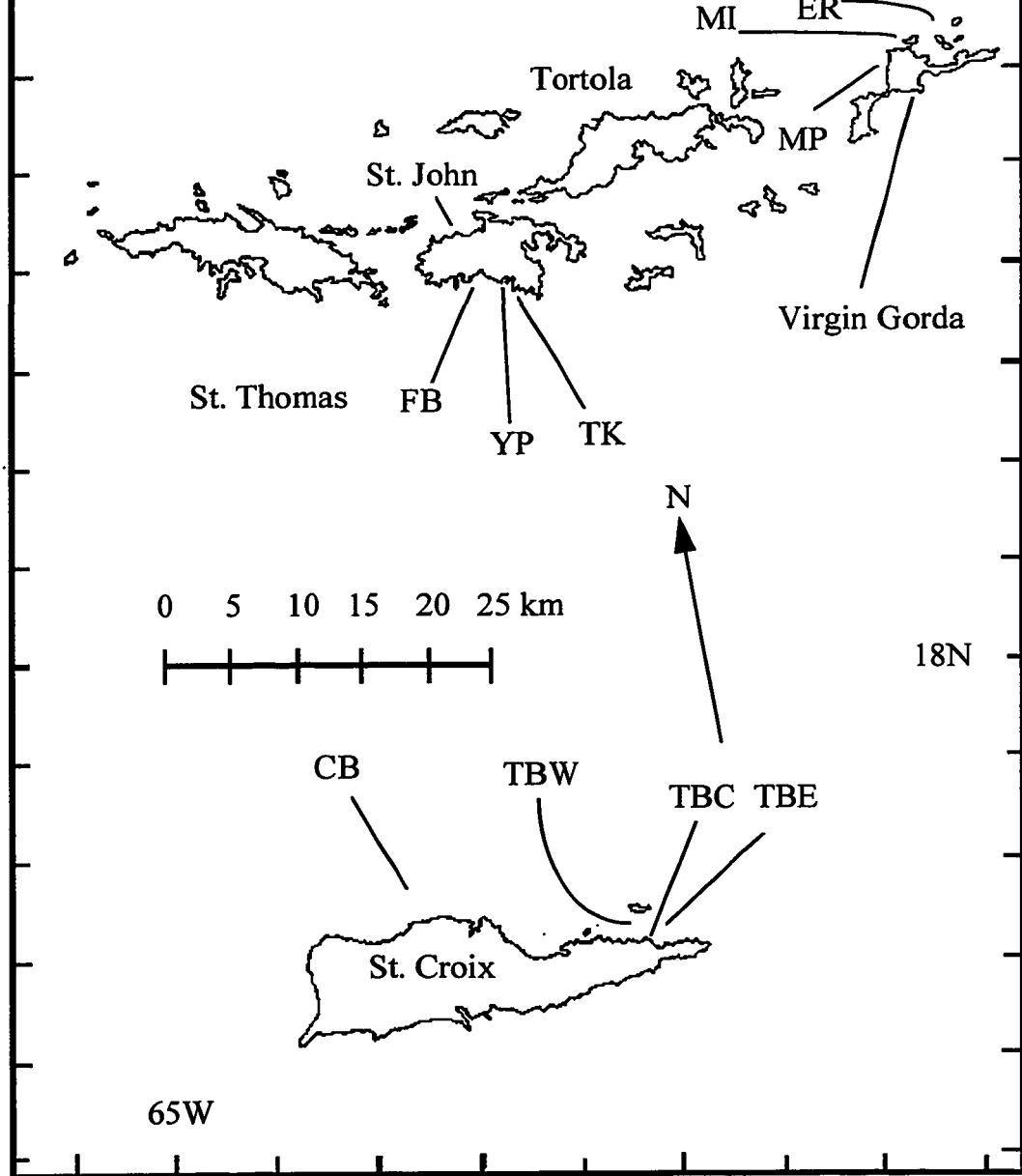


Figure 3.1. Locations of the study sites. TBE, TBC, TBW are Tague Bay east, central and west. CB = Cane Bay; TK = Tektite; YP = Yawzi Point; FB = Fish Bay; ER = Eustacia Reef; MI = Mosquito Island; MP = Mountain point.

My first objective was to determine at what spatial scale *S. viride* used the reef substratum. I used 10-minute focal animal observations and a longer term fin-clipping study to estimate movement rates of newly recruited *S. viride*. On the back reef, I followed focal animals for 10 minutes ($n = 27$). I marked the boundaries of the area the individual used by dropping hardware nuts with orange flagging tape tied through the hole. I did not mark the boundaries until the individual had moved away so as not to disturb the fish. Instead, I used natural habitat characteristics (specific corals) to keep track of the boundaries until I was able to place a marker. At the end of the observation period, I measured the length and width of the area used by the recruit, as well as the perimeter. I calculated the area for each observation based on the geometric shape it most closely resembled (triangle, square, circle, etc.).

To determine the fidelity of *S. viride* recruits to specific locations over a longer period of time (10 days), I conducted a fin clipping study on the fore reef slope at 5-7 m depth. I haphazardly collected 12 *S. viride* recruits (standard length = $40.5 + 9.6$ SD; range 27.5-62.5). Each fish was measured (mm SL), given a unique fin clip on the dorsal, caudal, or anal fins, and released at the location where first seen. I then placed an orange marker flag at this point. Every five days, I returned to the area and searched for each fish in the vicinity of its marker flag. When I found a marked fish, I recorded its presence and estimated the distance to its marker flag in half-meter increments. I continued this study for 10 days (15 July-25 July 1995), after which it became difficult to discern fin clippings. I did not use subcutaneous fluorescent markings or other brightly

over a two to three day period (Tolimieri, unpublished data). *Sparisoma viride* is somewhat cryptic as a juvenile so bright colored markings may have increased predation rates on recruits. This high rate of disappearance cannot be attributed to damage suffered from the actual marking because all individuals (n = 23) survived when kept in aquaria for three days (Tolimieri, unpublished data).

Recruitment within habitats

To determine whether microhabitat characteristics affected the distribution of *Sparisoma viride* at small spatial scales (within habitats), I compared the microhabitat characteristics of 1.0 m² quadrats occupied by *S. viride* recruits to randomly sampled null quadrats. To sample *S. viride* quadrats, I swam parallel to the reef at 5-6 m depth on the reef slope. When I spotted an *S. viride* recruit, I centered a 1.0 m² PVC quadrat at the point where I first saw the recruit and recorded the substrata present under 49 points within the quadrat (a 7 x 7 grid). These points were defined by intersecting monofilament lines. To sample null quadrats, I returned along the path I had followed while sampling *S. viride* recruits and dropped the quadrat after a pre-determined, random numbers of kicks. The quadrat was dropped from approximately two meters above the substratum. I sampled 20 *S. viride* and 20 null quadrats. The following four substratum categories were analyzed statistically: *Porites*, *Montastrea*, massive rubble, and *Acropora* rubble. The first two groups included both living and dead forms of the corals *Porites porites*, and *Montastrea annularis*. *Porites porites* (common name: club finger coral) produces

Massive rubble includes coral rubble derived from other boulder building corals such as *Siderastrea*. *Acropora* was rubble defined as dead *A. palmata*, a large branching coral that produces thick branches. Cochran's tests ($p < 0.05$) indicated that variances were heterogeneous so data were arcsine transformed prior to analysis to homogenize variances (Winer et al. 1992).

I used multivariate analysis of variance (MANOVA) followed by step-down analysis to compare *S. viride* and null quadrats (Tabachnick and Fidell, 1989). If *S. viride* quadrats differ from randomly sampled quadrats, this indicated that *S. viride* recruits associated with some substratum more or less than would be expected at random. MANOVA tests for an overall difference in the substratum characteristics between the two quadrat types, while step-down analysis attempts to indicate which substrata varied between treatments. In step-down analysis, priorities are assigned to the dependent variables (DV) (here substrata), and the highest priority DV is tested with univariate ANOVA. The remaining DV's are then tested with analysis of covariance (ANCOVA) with the first priority DV as the covariate. ANCOVA's determine whether the quadrats differed in individual substrata when variation in the first DV is accounted for by its use as a covariate. Ranking is based on theoretical considerations and alpha values must be adjusted for the number of tests done in the step-down analysis (Tabachnick and Fidell 1989). Because *S. viride* recruits appeared to associate with *Porites*, I ranked this DV first. Because I tested four DV's, the adjusted p-value for rejection of the null hypothesis in the step-down analysis is $p < 0.0125$.

To examine the effects of habitat and microhabitat characteristics on the medium scale recruitment of *S. viride*, I quantified abundance of recruits and the percentage cover of both live and dead *Porites* (live + dead, as above) at three sites (east, central and west) along the Tague Bay reef at the beginning of August 1994 and 1995. At each site, I enumerated recruit abundance in four habitats: back reef, reef crest, reef slope, reef base. In 1994, I did not sample the reef slope.

I used 30 x 2 m band transects to quantify *S. viride* recruitment and the percent cover of *Porites*. Specific methods are described in Sale et al. (1984b) and Tolimieri 1995. Briefly, a diver swam out a 30 meter transect tape. After waiting five minutes, the diver returned along the transect tape and recorded all *S. viride* recruits within 1.0 m of either side of the line. This distance was delineated by a T-shaped PVC bar 1.0 m wide. This PVC bar also contained 1.0 cm markings to aid in estimating fish sizes (i.e., less than 4.0 cm). A second diver then followed and recorded the substratum present under 120 points along the transect line (every 25 cm). As the quadrat study indicated that *Porites* influenced the small scale recruitment of *S. viride*, only the percent cover of *Porites* is reported here. Ten transects were sampled at each site.

I used a two-factor, mixed model analysis of variance (ANOVA) to determine if recruitment varied among habitats in 1995. In the ANOVA, site was a random factor, and habitat was a fixed factor. Because I did not sample the reef slope in 1994, I performed a separate ANOVA for the combined 1994-1995 data. Here I used a 3-factor, mixed-model ANOVA. Habitat was treated as a fixed factor. Year and site were both

0.05) indicated that variances were not homogeneous (Winer et al. 1992). Because I performed two statistical tests on the same data, the p-value to reject the null hypotheses of no difference was $p < 0.025$ for both ANOVA's and post-hoc Tukey's tests. I used regression analysis to determine whether the percent cover of *Porites* predicted or explained variation in *S. viride* recruitment among sites in the four habitats. I used mean values of recruitment, and *Porites* cover at each site in the analyses and years were analyzed separately. Therefore, each site contributes one datum to the analysis in each year. I used mean values to determine whether substratum characteristics explained differences among sites in mean abundance of recruits. Use of the raw data would have examined this relationship at the transect level (i.e. within sites). Visual examination of residuals suggested that variances were normally distributed and homogeneous (Zar, 1984).

Recruitment among sites

To determine whether recruitment of *S. viride* was correlated with the percent cover of *Porites* at a large spatial scale, I quantified recruitment during late July from 1991-1994 at 10 sites located on three islands: St. Croix, St. John and Virgin Gorda (Fig. 3.1). On St. Croix, there were three sites on the Tague Bay reef (east, central and west sites) and one site at Cane Bay. At St. John, recruitment was quantified at the former Tektite Project site, Yawzi Point and Fish Bay. At Virgin Gorda, recruits were censused at Eustacia Reef, Mosquito Island and Mountain Point.

Bay site was a fringing reef with spur and groove structure located on the northwest end of the island. The reef began at approximately 8 m and at the study site continued to approximately 13 m, where there is a steep vertical drop-off. Dead boulder coral and coralline pavement made up a greater portion of the substratum than at the Tague Bay sites. At the first two St. John sites, most of the structure was provided by underlying basaltic boulders encrusted by sponges, corals and gorgonians. The slope of the reef at these two sites was steeper than the other sites. Fish Bay, however, was a more exposed fringing reef with spur and groove development. The base of all three sites was at approximately 10-15 m. Eustacia reef on Virgin Gorda was a bank barrier reef and the substratum was similar to the Tague Bay sites. The Mosquito island site had high cover of soft corals and sea fans. *Montastrea annularis* was more common at Mountain Point than at other sites. These sites are more fully described in Tolimieri (1995).

Methods for quantifying recruit abundance followed those used to quantify recruitment among habitats (see above). However, I used 30 x 1 m transects, and 16 transects were done at each site. Along these transects, I also recorded the substrata present under 120 points along the transect line in the same manner as described above. Although several substratum types were recorded, I present only the percent cover of *Porites*.

I used regression analysis to determine whether variation in *S. viride* recruitment to these 10 sites was explained by the percent cover of *Porites* (live + dead, as above). I used mean values of recruitment and mean abundance of *Porites* on 16 transects at each

regression in each year. Years were analyzed separately (n=9 for 1991, n= 10 for 1992, 1993 and 1994). Visual examination of residuals suggested that variances were normally distributed and homogeneous (Zar 1984).

Abundance of adult *S. viride* was also recorded at these 10 sites in 1991 and 1993 on separate 30 x 1 m transects (n = 5-6). Adults were not censused at Mountain Point and the central Tague Bay site in 1991. I used correlation analysis to determine whether there was an association between recruitment and concurrent adult density. I performed correlation instead of regression analysis because I had no *a priori* reason to designate one variable the dependent variable. Recruit abundance may predict adult abundance, but the presence of adults may also enhance settlement. However, I used one-tailed hypothesis tests to test the *a priori* hypothesis that there was a positive correlation between recruit and adult abundance. Note that this *a priori* assumption does not affect the regressions that I performed in previous analyses. The hypothesis test is normally one-tailed (Zar 1984).

Results

Post-settlement movements

Focal animal observations conducted on continuous reef on the back reef showed that *Sparisoma viride* recruits used only small areas over the 10 minute observation ($1.2 \text{ m}^2 + 0.23 \text{ SE}$, n = 27). Of the 12 recruits that I fin-clipped between 14 and 15 July, nine

Table 3.1. Persistence of 12 fin-clipped fish on the fore reef slope. Fish were fin clipped on 14 June 1995 (10 fish) and 15 June 1995 (2 fish).

Distance from capture/release site	# of fish/date	
	20 June 95	25 June 95
0 - 0.5 m	5	1
0.6 - 1.0	1	6
1.1 - 1.5	3	2
1.6 - 2.0	1	1
2.1 - 2.5	0	0
2.6 - 3.0	0	1
3.1 - 3.5	0	0
3.6 - 4.0	1	0
Total	11	11

were identified within 1.5 m of their original tagging location on 20 July (Table 3.1). On 25 July, I found a total of 11 fin-clipped fish, nine of which were still within 1.5 m of their original tagging location. One fish was accidentally released approximately 7 m from the area where I first saw it, but later it returned to its original location and remained within 2.0 m of that point for the duration of the experiment. These results suggest that 1.0 m² quadrats sampled a sufficiently large area to characterize microhabitat use by *S. viride* recruits.

Multivariate analysis of variance indicated that *S. viride* quadrats and null quadrats differed significantly in their substratum characteristics (Pillai Trace = 0.396; df = 4, 39; $F = 6.387$; $p < 0.001$; Fig. 3.2). Step-down analysis indicated that *Porites* cover was higher in *S. viride* quadrats than in null quadrats (ANOVA; df = 1, 42; $F = 19.185$; $p < 0.001$, Fig. 3.2). Total *Montastrea* (ANCOVA; df = 1, 41; $F = 5.178$; $p > 0.0125$), *A. palmata* rubble (ANCOVA; df = 1, 14; $F = 1.22$; $p > 0.0125$) and massive coral (ANCOVA; df = 1, 41; $F = 0.920$; $p > 0.0125$) did not differ between quadrats when I accounted for variation in quadrats due to *Porites*.

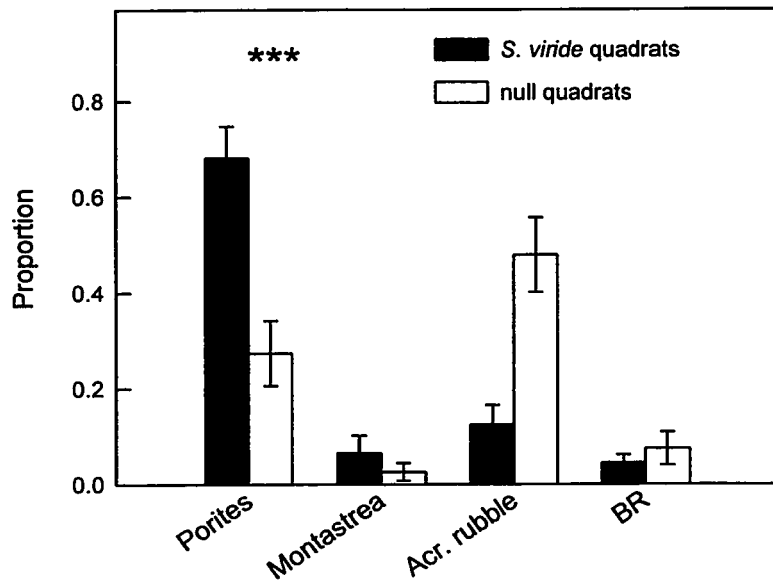


Figure 3.2. Mean proportional cover of four substratum types in *S. viride* and null quadrats on the fore reef slope of the Tague Bay Reef. TP = *Porites* (live + dead); TM = total *Montastrea*; AR = *Acropora* rubble; BR = other massive rubble; *** = $p < 0.001$ from the step-down analysis. Error bars indicate ± 1 SE.

Figure 3.3a,b shows the abundance of recruits in three of the four habitats for

1994 and all four habitats in 1995. ANOVA showed that from 1994-1995 recruitment

Table 3.2a. Results of 3-factor mixed-model ANOVA on recruitment of stoplight parrotfish to three habitats at three sites on the Teague Bay reef for 1994 - 1995. The habitats included in the analysis are: back reef, reef crest, fore reef base. Habitat (H) is a fixed factor. Year (Y) and site (S) are random factors. $p < 0.025$ to reject the null hypothesis.

source	df	MS	F	p
H	2	20.03	45.11	<0.001
S	2	1.82	4.54	0.18
Y	1	0.37	0.93	0.44
HS	4	0.32	2.84	0.17
YH	2	0.62	5.48	0.07
YS	2	0.40	1.64	0.20
YHS	4	0.11	0.46	0.77
error	162	0.246		

Table 3.2b. Results of 2-factor mixed-model ANOVA on recruitment of stoplight parrotfish to four habitats in three sites in August 1995. Habitats included in the analysis are: back reef, reef crest, fore reef slope, and fore reef base. Habitat (H) is a fixed factor. Site (S) is random. $p < 0.025$ to reject the null hypothesis.

Source	df	MS	F	p
H	3	22.11	13.69	0.004
S	2	3.04	12.60	<0.001
HS	6	1.62	6.69	<0.001
error	108	0.24		

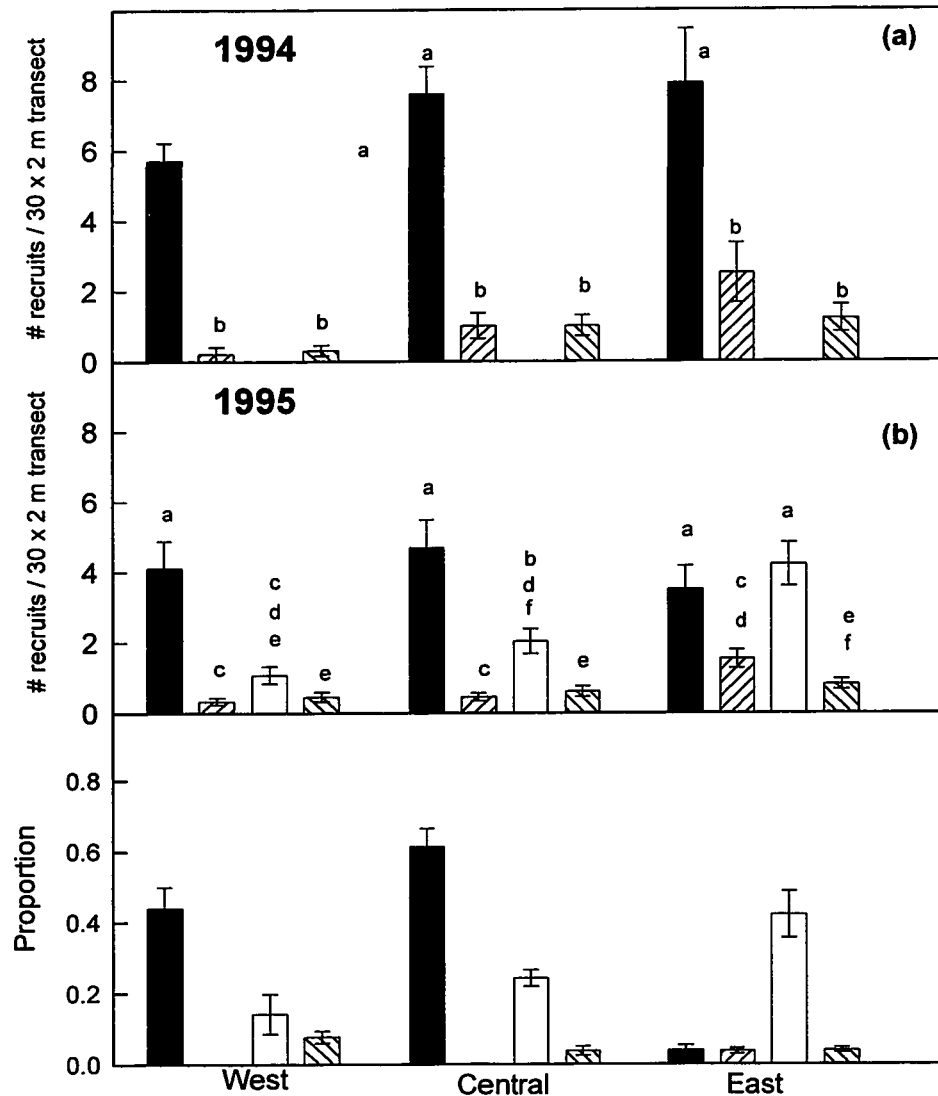


Figure 3.3. Mean recruitment of *S. viride* in four habitats on the Tague Bay Reef: (a) summer 1994 (b) summer 1995; (c) mean proportional cover of *Porites* in each habitat. The reef slope was not censused in 1994. Error bars indicate + 1SE. Letters indicate sites that could not be distinguished statistically by Tukey's HSD, $p < 0.05$. Black bars = back reef; hatched descending left = reef crest; white = reef slope; hatched descending right = reef base.

methods) indicated that recruitment was significantly higher to the back reef than to the reef crest or reef base.

When 1995 recruitment was examined both main effects (habitat, site) tested as significantly different, as did the interaction between the two (Table 3.2b). Tukey's HSD test ($p < 0.025$) indicated that in general recruitment was higher to the back reef than to the reef crest, reef slope, and reef base. Recruitment was also higher to the reef slope than to the reef crest and reef base. However, several exceptions occurred. Recruitment did not differ significantly between east reef slope and the back reef sites. Likewise, the central reef slope and east back reef did not differ in recruitment of *S. viride*. The west reef slope did not differ from the reef crest in recruitment, and central reef slope received the same amount of recruitment as the east reef crest. Finally, the west reef slope did not differ from any of the reef base sites, and the central reef slope did not differ from the east reef base. The only variation among sites was among reef slope sites. The east reef slope received higher recruitment than both the central and west reef slope.

At this medium spatial scale, regression analysis indicated that the percent cover of *Porites* explained 45% of the variation among sites in mean *S. viride* recruitment in 1994 (Fig. 3.4, $n = 9$, $r^2 = 0.45$, $p = 0.048$). In 1995, *Porites* cover explained 74% of the variation in mean *S. viride* recruitment ($n = 12$, $r^2 = 0.74$, $p < 0.001$). Mean percent cover of *Porites* is shown in Figure 3.3c. In both years, the east back reef site was an outlier (Studentized residual: 1994 = 7.824; 1995 = 5.436). Although it had low percent cover of

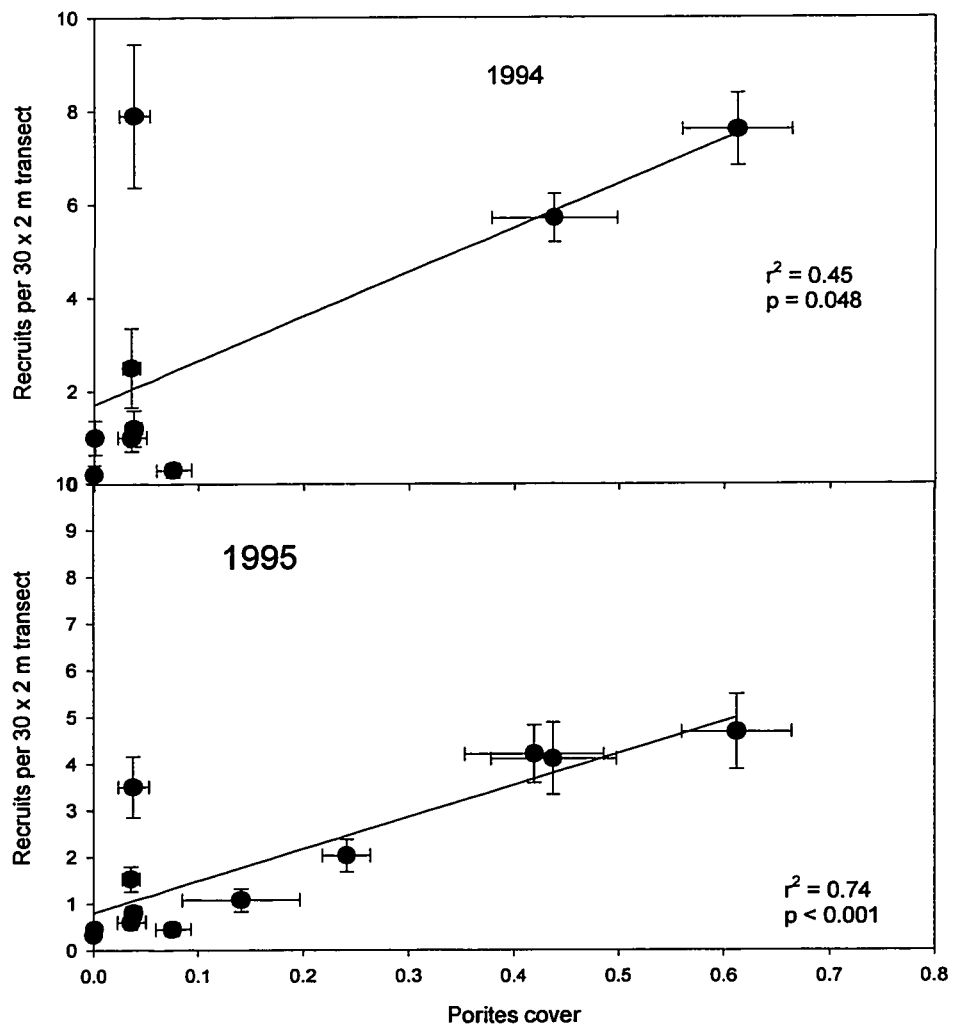


Fig. 3.4. Results of regression analysis showing the relationship between mean *S. viride* recruitment and *Porites* cover around the Tague Bay reef at 9 sites in 1994 and 12 sites in 1995. Error bars indicate ± 1 SE.

Porites, it still received high recruitment. If this site is excluded from the analysis, the *Porites* distribution explained 93% of the variation in mean *S. viride* recruitment among

11, $r^2 = 0.935$, $p < 0.001$).

Large scale recruitment variation

Regression analysis showed that the percent cover of *Porites* explained 66-81% of the variation among sites in mean recruit abundance among the 10 sites located on St. Croix, St. John and Virgin Gorda in three of the four years from 1991 - 1994 (Fig. 3.4a-d).

In 1991, there was no relationship between adult and juvenile distribution among sites ($n = 8$, $r = 0.463$, $p > 0.05$, Fig. 3.5). However, in 1993 recruit and adult abundance were correlated ($n = 10$, $r = 0.537$, $p < 0.05$). When data were pooled across years, there was a significant correlation between recruit and adult abundance ($n = 10$, $r = 0.881$, $p < 0.0005$, Fig. 3.5).

Discussion

The results of this study indicate that microhabitat characteristics influence the recruitment of *Sparisoma viride* across several spatial scales. At small spatial scales (1.0 m² quadrats/within site) stoplight recruits associated with *Porites*. At a medium spatial scale, *Porites* cover explained 45-74% of the variation in mean recruit abundance at 12 sites located in four habitats. When one site was excluded, over 90% of the variation in *S. viride* recruitment was accounted for by *Porites* distribution. This association between recruit abundance and *Porites* cover continued to 'scale up' and predicted recruitment

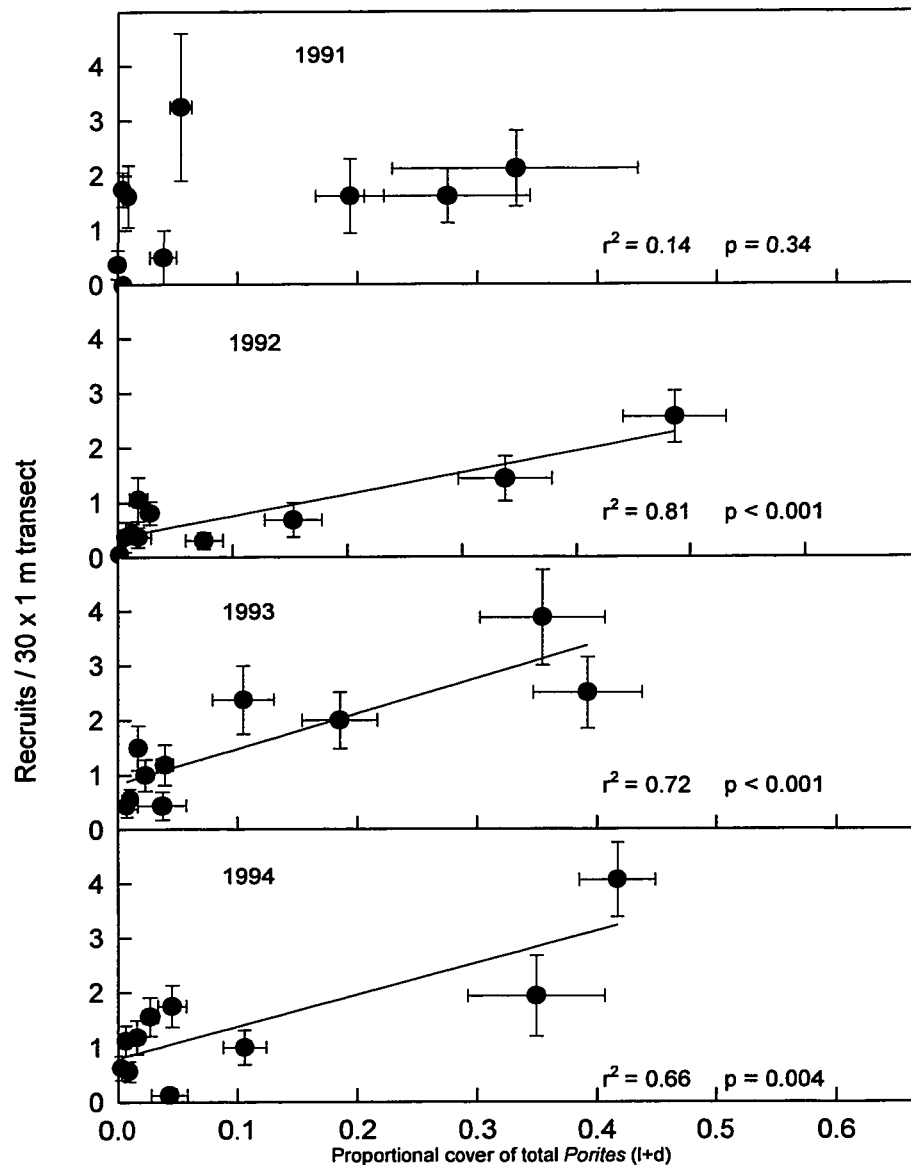


Figure 3.5. Relationship between mean *S. viride* recruitment and mean proportional cover of *Porites*. Error bars indicate ± 1 SE.

among sites on different islands. These sites were separated by 70+ km. Additionally, this study showed a correlation between the pattern of recruitment and the contemporary

interesting because they demonstrate that processes that operate at small spatial scales (within sites) can influence distribution and abundance at larger scales as well. More specifically, these results indicate that the make-up of local patches may affect the rate at which those patches are replenished.

Small spatial scale microhabitat use

Sparisoma viride recruits were associated with both live and dead *Porites* more than would be expected at random. Selection and/or use of specific microhabitats is well documented for newly recruited juvenile fishes in both temperate marine systems (Levin 1991, 1993, 1994a Carr 1991; Garcia-Rubies and Macpherson 1995; Levin and Hay 1996) and on coral reefs (Eckert 1985; Sale et al. 1984a; Booth 1992; Eggleston 1995; Tolimieri 1995). For example, Levin (1991, 1993) showed that recruitment of the temperate wrasse *Tautogolabrus adspersus* was higher to areas with foliose algal cover than to areas with only crustose algae. Carr (1991) found that nine species of rockfish (Scorpaenidae, genus *Sebastes*) showed strong and distinct habitat selection based on substratum type, algal type, relief, and depth. Booth and Beretta (1994) showed preferences for live coral by several Caribbean pomacentrids. Similar results are found in studies of Australian reefs (Sale et al. 1984a) and the Mediterranean (Garcia-Rubies and Macpherson 1995).

Researchers have suggested that use of specific microhabitats is important for avoiding aggression from adults (Sale 1972a), avoiding predators (Shulman 1984; Hixon

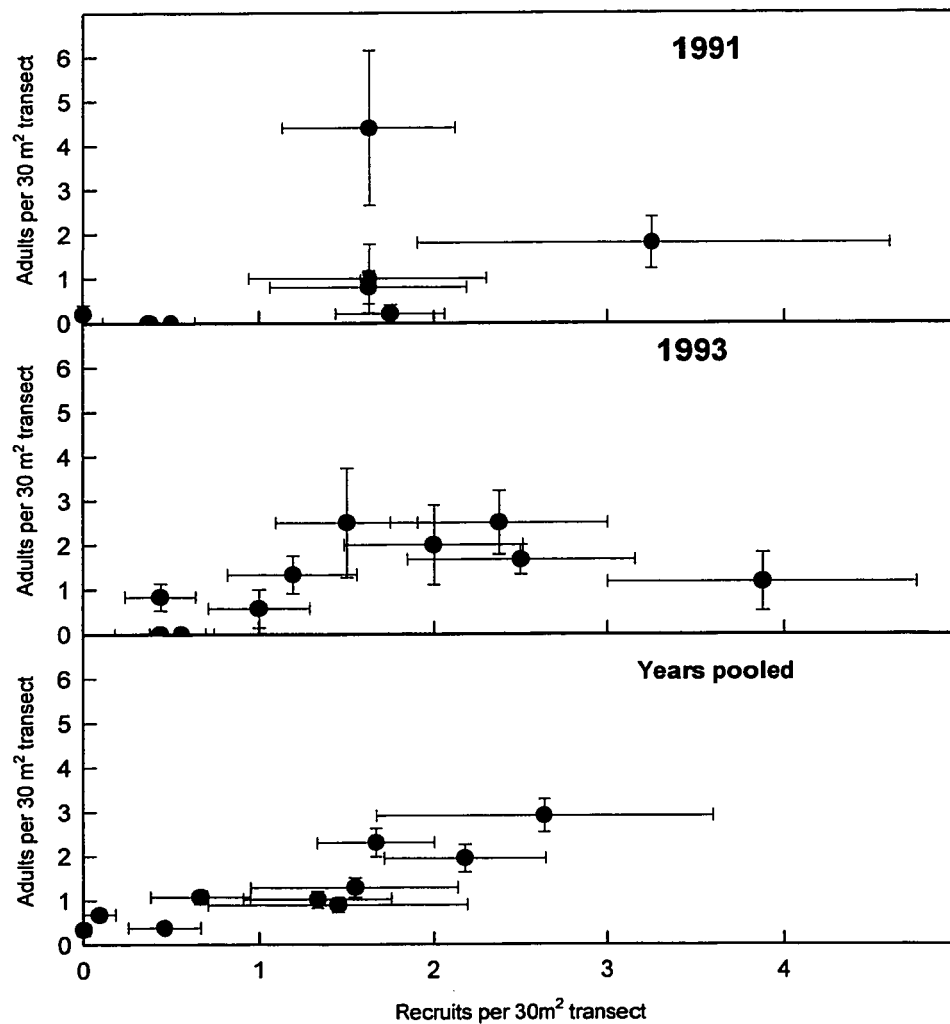


Figure 3.6. Relationship between recruitment and adult abundance at 10 sites. Data are the mean recruitment and mean adult abundance at a site: (a) 1991, (b) 1993, (c) pooled across years. Error bars indicate ± 1 SE.

and Beets 1989, 1993), and obtaining food resources (Clarke 1992; Levin 1994a). I did not attempt to determine why *S. viride* recruits were associated with *Porites*. However, several non-mutually exclusive alternatives exist; shelter from predation and food

branches 15-20 cm long and 1-2 cm wide. On the Tague Bay reef, *P. porites* forms dense mono-specific stands, in which the branches are closely packed. This morphology should provide excellent shelter from larger predators when the recruits are newly settled and still very small. As fish grow larger, they develop more mobile behavior and these small shelter holes probably become less important. It is also possible that *Porites* in some way provides a higher quality food source for *S. viride* recruits. The close packing of the branches of *Porites* at these sites may prevent larger herbivores from grazing on the epiphytic algae growing on the dead portions of the branches. It is impossible to distinguish between these two hypotheses based on the data herein. *Sparisoma viride* recruits do receive a large number of aggressive attacks from territorial damselfishes (pers. obs.), and *Porites* may provide some sheltering function here.

Likewise, my data do not allow us to distinguish whether the association between *S. viride* recruits and *Porites* was established by microhabitat choice during settlement or some post-settlement process such as predation mediated via substratum type. Selection for certain microhabitat characteristics does occur during settlement (Sale et al. 1984a; Booth 1992; Tolimieri 1995). In the Caribbean, Tolimieri (1995) showed that *Stegastes planifrons* (Pomacentridae) selects the coral *Montastrea annularis* during settlement, and that this selection affects the distribution of recruits within habitats. Sale et al. (1984a) showed settlement preferences for several species of Australian reef fishes, and Sweatman (1985, 1988) showed that individuals chose to settle with resident conspecifics. On a slightly larger spatial scale, Wellington (1992) found that both choice

damselfishes to two habitats on the Tague Bay reef.

Recruitment among habitats

At a medium spatial scale, I also found a correlation between microhabitat characteristics and the mean abundance of *S. viride* recruits at several sites located in four different habitats. On the Tague Bay reef, *S. viride* demonstrated high recruitment to the back reef and slightly lower but still high recruitment to the reef slope. Recruitment to the deeper reef base and reef crest was much lower. This pattern of recruitment correlates well with the distribution of living and dead *Porites* in these habitats. Although *Porites* acted as a good predictor at this spatial scale, it is difficult to say whether *Porites* caused the pattern of recruitment. *Sparisoma viride* recruitment and *Porites* distribution were correlated, but both were also correlated with what appeared to be the general current direction. *Sparisoma viride* recruitment and *Porites* abundance may have been influenced by the same processes. Moreover, the high recruitment of *S. viride* at the east back reef site coupled with the low percent cover of *Porites* at that site suggests that habitat (not microhabitat) related variables also may be important at this scale. Several authors have shown that habitat can affect recruitment and the distribution and abundance of adults (Wellington 1992; Green 1996). Factors such as current speed, wave action and entrainment of larvae on the back reef may be important in addition to the abundance of *Porites* (Victor 1983, 1986; Leis 1991, 1994; McGehee 1994). There is evidence that larval supply via currents may be important in influencing recruitment (Victor 1983,

a good predictor of *S. viride* abundance at this spatial scale.

Recruitment at large spatial scales

In chapter 2, I examined recruitment in 14 species of Caribbean reef fishes at the same 10 sites as in the present study. Six of the 14 species, including *S. viride*, demonstrated spatial patterns of recruitment that were concordant across years (1992-1994). Absolute numbers of recruits arriving each year varied, but the ranking of sites remained the same from year to year. All species did not show the same ranking of sites. The data from the present study suggest that the consistent spatial pattern of recruitment shown by *S. viride* was the result of some interaction with the microhabitat characteristics of the local patches. *Sparisoma viride* recruits were associated with *Porites* within sites, and this association explained variation in recruitment among the 10 large spatial scale sites in three of the four years. It is possible that the consistent recruitment patterns were the result of some other process such as self-recruitment (Leis 1994), or larval supply as influenced by current regimes (e.g. Sponaugle and Cowen 1996; Caselle and Warner 1996). *Porites* distribution and *S. viride* recruit abundance may also be influenced by the same processes, but *S. viride*'s use of *Porites* at small spatial scales supports the conclusion that the large scale recruitment pattern was influenced by *Porites* distribution.

The results of the present study offer an interesting contrast to both Tolimieri (1995), and Caselle and Warner (1996). Tolimieri (1995) examined the relationship between microhabitat characteristics and recruitment of the three-spot damselfish,

with the coral *Montastrea annularis* at small spatial scales, but this association did not affect the recruitment of *S. planifrons* among sites. However, there was little variation in the abundance of *M. annularis* among sites (range 0-15% cover), while here the percent cover of *Porites* was much greater at some sites than at others (range 0-45% cover). Lack of an association between *M. annularis* and *S. planifrons* may have been due to the low variation of *M. annularis* among sites. Likewise, Caselle and Warner (1996) found that microhabitat characteristics influenced the recruitment of the bluehead wrasse, *Thalassoma bifasciatum*, within sites, but that habitat characteristics did not predict the pattern of recruitment among sites. Instead, recruitment among sites appeared to be related to physical oceanographic processes. Interestingly, the recruitment patterns of *S. viride* and *T. bifasciatum* along the north shore of St. Croix are the opposite with high recruitment of *T. bifasciatum* on the west end of the island and high recruitment of *S. viride* on the east end of the island. Therefore, although oceanic processes may influence the recruitment of both species (as well as *Porites* distribution), these results indicate that such processes may not influence all species in the same way.

It is important to determine the nature of the relationship between recruitment and adult abundance (Doherty 1983, 1991; Doherty and Fowler 1994a,b) because if the relationship is linear, this suggests that local populations are recruitment limited and that post-recruitment, equilibrial processes (such as competition for food) do not greatly influence adult abundance. Conversely, if there is a density-dependent relationship between recruitment and adult abundance, this suggests that equilibrial, reef based

dynamics. A non-linear relationship should not be taken as proof of density-dependent regulation of population size, however, because variable mortality and variable recruitment in conjunction with the life-span of the organism can obscure the relationship (Warner and Hughes 1988).

Work done by Victor (1983, 1986) in Panama and Doherty and Fowler (1994a,b) on the Great Barrier Reef (GBR) has shown that recruitment can determine adult abundance over large spatial scales (1 km-10's of km). For example, Doherty and Fowler (1994a,b) found that previous recruitment history explained almost 90% of the variation in adult abundance of *Pomacentrus moluccensis* among reefs separated by up to 70 km. *Sparisoma viride* recruitment showed a consistent spatial pattern across years, and this pattern of recruitment was explained by the percent cover of *Porites*. Adult distribution was correlated with recruitment patterns both within and across years. It is tempting to conclude that *S. viride* populations in this study are recruitment limited and that the interaction between microhabitat characteristics and recruitment influences the distribution and abundance of the adult population. However, such conclusions cannot be drawn from the present data because recruitment and adult abundance were quantified during the same time period. It is impossible to know whether the recruitment patterns observed from 1991 - 1994 will result in similar adult distributions in the future. My data do show that sites that received high recruitment relative to other sites also supported higher adult abundance. Longer term monitoring would be required to determine whether *S. viride* adult distribution is the result of previous recruitment history. I think it unlikely

other substrata (Chapter 5). If adult populations are limited by recruitment patterns, this suggests that juvenile substratum requirements may determine the distribution and abundance of adults.

Conclusions

Many studies have focused on whether processes that are influenced by the local reef environment-processes such as microhabitat choice, or interactions with resident fishes during settlement-affect the rate of recruitment to that local patch (Doherty 1983; Sweatman 1985, 1988; Booth 1992; Booth and Beretta 1994). Microhabitat choice (Sale 1972b; Sale et al. 1984a; Booth 1992; Tolimieri 1995), and interactions with resident fishes (Sweatman 1985, 1988; Booth 1992) have been shown to influence the rate of recruitment of juvenile fishes, and their distribution on the reef. However, most studies on coral reefs have considered only small spatial scale interactions and have not attempted to determine if these processes influence recruitment at larger spatial scales (but see Tolimieri 1995; Caselle and Warner 1996).

Here, I have shown that *S. viride* recruitment is correlated with the abundance of the coral *Porites* across several spatial scales. Patterns of microhabitat use determined at a small spatial scale (1.0 m²) predicted recruitment among habitats and among sites on different islands. High recruitment sites also supported higher adult populations than low recruitment sites. These results are interesting because they indicate that the local reef environment may influence the replenishment of demersal fish populations. These results

et al. 1995) need to take into account the characteristics of both the fish species and the reefs that they attempt to manage.

DAMSELFISH ON THE SETTLEMENT AND RECRUITMENT OF THE STOPLIGHT PARROTFISH

Abstract

Recruitment often plays an important role in the population dynamics of marine organisms. Because recruitment includes settlement plus a short period of time in the benthic habitat, estimates of recruitment can be affected by both pre- and post-settlement processes. I conducted a series of experiments on 2.0 m² patch reefs to examine the importance of pre- and post-settlement processes to the distribution and abundance of recruits of the stoplight parrotfish, *Sparisoma viride*, on the Tague Bay reef, St. Croix, U.S.V.I.. Stoplights settled in higher numbers to patch reefs that contained resident stoplight recruits, and persistence was higher at higher stoplight densities. Resident damselfish directed significant amounts of agonistic behavior towards newly settled stoplight parrotfish. Damselfish presence had no effect on stoplight settlement, but it did reduce stoplight recruitment. Natural densities of stoplight recruits were significantly higher on the coral *Porites porites* than on another common coral *Montastrea annularis*, but I did not detect differences in settlement to these two substrata. A patch reef experiment demonstrated that recruitment differed between the two substrata. Analysis of the size classes of recruits present on *P. porites* and *M. annularis* patch reefs in this experiment suggested that differences in recruitment were established after settlement. These results demonstrate that both pre- and post-settlement processes influence the

recruitment patterns can be altered from initial settlement patterns.

Introduction

Many marine organisms have complex life-cycles, in which a planktonic larval stage is followed by demersal or site attached juvenile and adult stages (Thorson 1950; Breder and Rosen 1966; Sale 1980; Roughgarden et al. 1988). The population dynamics of these species can be influenced by very different processes at different times in the life-cycle. During the planktonic stage, oceanographic processes can control the supply of larvae to locations at larger scales (Shanks and Wright 1987, Roughgarden et al 1988; Leis 1991; Sponaugle and Cowen 1996, Richards et al. 1995). During settlement (movement from the water column to the benthos), individuals may choose or be excluded from settlement sites (Sweatman 1985; 1988; Booth 1992; Sunderberg and Kennedy 1993; Tolimieri 1995; Danilowicz 1996; Doherty et al. 1996; Morgan et al. 1996). Finally, predation, competition, and interactions with other organisms of the same or other species can influence the growth, distribution and abundance once recruits are in the benthic habitat (Underwood and Denley 1984; Menge and Sutherland 1987; Underwood and Fair-weather 1989; Jones 1991; Carr and Hixon 1995; Forrester 1995; Robertson 1995, 1996).

Recruitment can be a significant factor in the population dynamics of marine organisms (Roughgarden et al. 1988; Doherty and Fowler 1994a,b). Here I quantify 'recruitment' as the time at which a newly settled fish is first observed in the adult habitat

researchers have found strong correlations between recruitment and adult population size, suggesting that adult populations may be limited by low levels of recruitment instead of factors like competition in the benthic habitat (Victor 1983, 1986; Doherty and Fowler 1994a,b). Note, however, that when counted, recruits have been on the reef from several days to several months. Therefore, recruitment patterns have the potential to be altered from initial settlement patterns by processes like competition, predation and movement of individuals. Since recruitment often has strong effects on the population dynamics of marine organisms, it is necessary to understand the relative importance of factors operating during and after settlement in determining recruitment patterns.

For reef fishes, workers have shown that during settlement individuals may actively choose between different habitats or substrata (Sale et al. 1984a; Wellington 1992; Booth 1992; Meekan et al. 1995; Tolimieri 1995; Danilowicz, 1996). They may settle in greater numbers with resident conspecifics (Sweatman 1985, 1988; Booth 1992, 1995), but resident fish can also reduce settlement of other species (Sweatman 1985). Once fish are on the reef, their persistence (mortality + migration) or growth rates may differ among substrata or habitats (Jones 1988; Wellington 1992; Tolimieri 1995). Recruits may suffer reduced growth as a result of intra- or interspecific competition, but survival can also be higher in larger group of conspecific recruits (Booth 1995) or in the presence of adults (Forrester 1990, 1991). Recent work has shown that interspecific competition may limit adult abundance (Robertson 1995, 1996) and that early post-settlement mortality may be density-dependent (Tupper and Hunte 1994; Schmitt and

recruitment. For most species, mortality is highest during the first few days or weeks after settlement, and workers have demonstrated large spatial and temporal variation in mortality rates (Aldenhoven 1986; Eckert 1987; Shulman and Ogden 1987; Jones 1991; Booth and Beretta 1994).

There is usually good correspondence between settlement and subsequent recruitment patterns (Milicich et al. 1992; Wellington 1992; Williams et al. 1994; Levin 1996), and the choices made by larvae during settlement generally have consequences during the post-settlement stage. For example, Wellington (1992) showed that persistence of damselfish recruits was higher in habitats where they settled in higher numbers. However, this is not always the case (Levin 1993), and benthic processes may confound and alter the settlement/recruitment relationship (Jones 1991; Levin 1993; Booth 1995).

Most of the work on pre- and post-settlement processes in coral reef fishes has been done on damselfish (Pomacentridae) partly because they are abundant and easy to manipulate (Doherty 1983; Jones 1987a,b, 1988a, 1990, 1991; Forrester 1990, 1991; Booth 1992, 1995; Booth and Beretta 1994; McGehee 1995; Tolimieri 1995, Robertson 1996, but see Victor 1983, 1986; Shulman and Ogden 1987; Robertson 1988a,b,c; Forrester 1995). This work forms the basis for our understanding of the population and community dynamics of reef fishes, but it is limited to one family of fishes whose species are aggressive, territorial, and have small home ranges (Sale 1971; Thresher 1976;

different results (Shulman and Ogden 1987, Robertson 1988a).

In this report, I examine the effects of: 1) substratum type, 2) conspecific density, and 3) damselfish presence on the settlement and recruitment of the stoplight parrotfish, *Sparisoma viride* (Scaridae). I determine whether patterns of recruitment related to these three factors are established at settlement or after fish have settled to the reef habitat.

Methods

Study species

The stoplight parrotfish is a common herbivore on Caribbean coral reefs, feeding on epiphytic algal turf, crustose coralline algae, and endolithic algae (Bruggemann et al. 1994a,b). It is a protogynous hermaphrodite (Reinboth 1968). Settlement to the reef occurs at approximately 8-10 mm standard length (SL) (Tolimieri pers. obs.). Fish mature at 170-270 mm SL and can attain lengths in excess of 500 mm. Sex change from female to male may occur at 150-250 mm SL (Koltes 1993). For the context of this study, I define recruits as juvenile fish <50 mm SL. These individuals are several days to several months old.

Study site and general methods

All field work was carried out on the back reef of the bank barrier reef at Tague Bay, St. Croix, USVI (17°46' N, 64°36' W). The back reef ranged in depth from 3-6 m at its base to partially emergent on the crest at low tide. Dead *Acropora palmata*, living

reef. Other hard corals such as *Siderastrea* spp., *Diploria* spp., *Agaricia* spp. and *Copophilia* spp. occurred but were less common. In some areas, there were patch reefs separated by sand. The lagoon floor consisted primarily of sand with sea grass beds located in particular areas.

I conducted the following experiments on patch reefs approximately 2.0 m². All fish collections were made using quinaldine and aquarium nets. Patch reefs were separated by 2 - 3 m of sand. When removing damselfish, I also used barrier nets. Some collections of damselfish were done on all reefs so that all reefs received some level of manipulation. Where required, collected damselfish were relocated or returned to their reefs.

Effects of coral type on settlement

In Chapter 3, I found that the percent cover of the coral *Porites porites* (hereafter *Porites*) influenced the distribution of stoplight recruits across a range of spatial scales. In the first study of this paper, I tested the hypothesis that stoplight recruits preferentially selected *Porites* at settlement. I selected 10 *Porites* patch reefs and 10 *Montastrea annularis* (hereafter *Montastrea*) patch reefs. I used a PVC tape measure to record the maximum length and width of each patch reef in order to estimate its area and convert counts of stoplight recruits to densities. I counted the number of stoplight recruits on each patch reef to determine whether natural recruit density varied between the two coral types. After counting the recruits, I removed all of the stoplight recruits from these patch

then removed all newly settled stoplight recruits (~ 8 - 10 mm SL). Settlers were collected from 20 July to 1 August, 1995 (5 days on either side of the new moon; when settlement appeared to be highest; Tolimieri pers. obs.). I used t-tests to determine whether (1) initial density and (2) total settlement density varied between the two coral types. Cochran's tests indicated that the data did not require transformation ($p > 0.05$ in both cases).

Effects of conspecifics and damselfish on settlement and recruitment

In a second experiment, I examined the effects of resident conspecifics and damselfish on settlement and recruitment. Initial pilot experiments indicated that although stoplight recruits had small home ranges (Chapter 3), it was not possible to transplant them to patch reefs as is often done with damselfishes (see for example Jones 1987a,b; Forrester 1990; Booth 1995; Tolimieri 1995). My attempts at transplanting recruits generally resulted in high rates of disappearance overnight or even within a few hours. These disappearances could not be attributed to mortality due to handling. I was able to collect recruits and keep them in aquaria overnight or for several days with negligible mortality (<5%) even when fish had been injected with fluorescent dye or tattooing ink (Chapter 3). Instead of transplanting recruits to set up treatments in the following experiment, I reduced densities from natural levels.

I selected 30 *Porites* patch reefs from a larger sample. These patch reefs were selected to have similar initial densities of stoplight recruits (0.8-1.2 recruits m^{-2}). Patch

(1) the presence and absence of damselfish, and (2) the density of stoplight recruits. I removed all the damselfish from half of all reefs ($n = 15$). Damselfish were not manipulated on the remaining reefs. Within each damselfish treatment, I removed all the stoplight recruits from five reefs, and half the stoplights from another five reefs. Stoplight densities on the remaining five reefs within each damselfish treatment were left at their initial densities. The densities of stoplights in the three treatments were approximately 0, 0.5 and 1.0 recruits m^{-2} .

To examine residency patterns of stoplight recruits, I collected 3-4 fishes from each patch reef and marked individuals with individual fin clips (dorsal, anal, and/or caudal fins). I searched for these fishes on 3 occasions over the next ten days to determine whether they had disappeared or remained on their original patch reefs. I did not search for the fishes for a longer period because previous studies (Tolimieri in press) indicated that after 10-14 days clipped fins re-grew and positive identification became difficult.

I visited each reef every other day and counted and removed all newly settled fish (recognized by their small size). Once a week, I removed any damselfish that had moved onto damselfish exclusion reefs. Likewise, I removed any parrotfish from the 0 density treatment. To maintain similar levels of disturbance on all reefs, I collected and then released at least one damselfish on the damselfish inclusion treatments. I did not manipulate stoplight density after the beginning of the experiment on the low and high density treatments. The experiment ran for 25 days from 5 June to 30 June, 1995, after

settlement. Percent change in density for resident fishes was calculated as the change in density from the first premanipulation census (denominator) to the final census (numerator).

To verify that damselfish and parrotfish interacted, I performed 10 minute focal animal observations on the stoplight recruits resident on the patch reefs. During these observations, I recorded (1) the number of bites and (2) the number of chases involving the focal individual. For each chase event, I recorded the species involved. I made 2-4 observations per replicate patch reef, but I calculated the average number of bites and aggressive encounters per replicate (reef) before analyzing the data since the patch reef was the replicate, not the individual fish.

I used a two-factor analysis of variance (ANOVA) to test whether conspecifics and resident damselfishes affected total settlement of stoplight parrotfish (calculated as the total density of settlers to each treatment). In the analysis, both factors were fixed. Data were $\ln(x+1)$ transformed prior to analysis to control for heterogeneity of variances. To determine whether conspecific density and presence of damselfish influenced the local density of stoplight recruits after settlement, I conducted a similar, separate ANOVA on the change in density of stoplight recruits. Stoplight exclusion treatments were not included in this analysis (they were maintained at 0 fish m^{-2}). Variances were homogeneous and did not require transformation prior to analysis (Bartlett's test, $F = 1.396$; $p = 0.243$). I analyzed parrotfish behavior in a two factor multivariate analysis of variance (MANOVA). Both factors (damselfish, parrotfish density) were fixed. When

determine whether bite rate or the number of chases differed between treatments.

Coral type, damselfish and recruitment

Data from the previous two experiments indicated that microhabitat choice did not occur during settlement, and I also failed to find an effect of damselfish on settlement and post-settlement changes in density (see results). I conducted a third patch reef experiment during the summer of 1996 to further explore the relationships between damselfish presence, coral type and recruitment. I performed this third experiment because my previous test for effects of damselfish had low power (see results), and to determine at size (here expressed as standard length) the difference in recruitment to *Montastrea* and *Porites* manifested (i.e., immediately following settlement or among larger fishes).

I selected 20 *Porites* and 20 *Montastrea* patch reefs on the back reef of the Tague Bay reef. I recorded the maximum length and width of each reef and removed all stoplight recruits from the reefs. I then removed damselfish from half of the reefs in each coral treatment. I visited each reef approximately once a week, recorded the number of stoplight recruits present on each reef, and removed damselfish from exclusion treatments. I did not remove stoplight recruits during the experiment. Again, to maintain similar levels of disturbance in all treatments, I tried to capture and release back on to the reef at least one damselfish on the damselfish inclusion treatments. I recorded the number of stoplight recruits in the following size classes: ≤ 10 mm SL; ≤ 15 mm SL; ≤ 20 mm SL; ≤ 30 mm SL; ≤ 40 mm SL; ≤ 50 mm SL. Size classes did not overlap (i.e. fish

estimated to be 10–15 mm SL when they first settled. I refer to these size classes simply as 10, 15, 20, 30, 40, and 50 mm. I carried a Plexiglas slate with 5 mm markings (up to 100 mm) to aid in estimating the length of the fishes and record data. This experiment ran for approximately one month from 10 June to 15 July, 1996. I used a two factor repeated measures ANOVA to determine whether damselfish presence and coral type affected total recruit density. Both factors were considered fixed factors, and the data were $\ln(x+1)$ transformed prior to analysis.

Results

Coral type and settlement

Prior to manipulation, *Porites* and *Montastrea* patch reefs contained a total of 63 recruits, and natural densities of stoplight recruits were significantly higher on *Porites* patch reefs than on *Montastrea* patch reefs (pooled variance t-test, $df = 18$, $t = 2.258$, $p = 0.037$, Fig. 4.1a). A total of 98 fish settled to the *Montastrea* and *Porites* patch reefs over the experiment, but total settlement density did not differ between the two coral types (t-test, $df = 18$, $t = 0.578$, $p = 0.571$, Fig. 4.1b) indicating that the difference in recruitment to the two coral types was not established at settlement.

Settlement, local density, conspecifics and damselfish

I collected a total of 173 settlers over the course of the experiment. Conspecific density significantly influenced stoplight settlement (ANOVA, $df = 2$, $F = 4.39$, $p = 0.02$, Fig. 4.2). This factor explained 23% of the variation in stoplight settlement. Settlement



Figure 4.1. (a) Mean natural density of *S. viride* recruits on two substrata at Tague Bay. (b) Total settlement density on the same patch reefs. Error bars indicate $\pm 1\text{SE}$. * = $p < 0.05$. NS = $p > 0.05$ (both from t-tests)

was significantly higher to high density ($\sim 1.0 \text{ fish m}^{-2}$) stoplight treatments than when stoplights were absent (Tukey's test, $p = 0.02$). The presence of damselfish did not

interaction between factors (ANOVA, $df = 2$, $F = 1.042$, $p = 0.37$). Although not significant, there was a trend of lower settlement when damselfish were present. The power of this experiment to detect an effect by damselfish on stoplight settlement was low ($1-\beta < 0.2$).

The percent change in resident stoplight density differed between low and high density stoplight treatments (ANOVA, $df = 1$, $F = 15.27$, $p = 0.001$, Fig. 4.3). Local density of stoplight recruits decreased at low stoplight densities. It remained the same or increased at high stoplight density. This relationship explained 47% of the percent change in stoplight recruit density. The presence of damselfish did not cause changes in local stoplight density (ANOVA, $df = 1$, $F = 0.29$, $p = 0.60$), and there was no interaction between factors (ANOVA, $df = 1$, $F = 1.27$, $p = 0.28$).

The behavior of stoplight recruits differed between treatments in which damselfish were present or absent (MANOVA, Pillai Trace = 0.763, $df = 2, 15$, $F = 24.14$, $p < 0.001$). Stoplights were involved in more chases when damselfish were present than when damselfish were absent (ANOVA, $df = 1, 16$, $F = 51.44$, $p < 0.001$, Fig. 4.4a), but there was no difference in bite rate (ANOVA, $df = 1, 16$, $F = 0.098$, $p = 0.758$, Fig. 4.4b). The majority of chases involved damselfish chasing stoplight recruits,

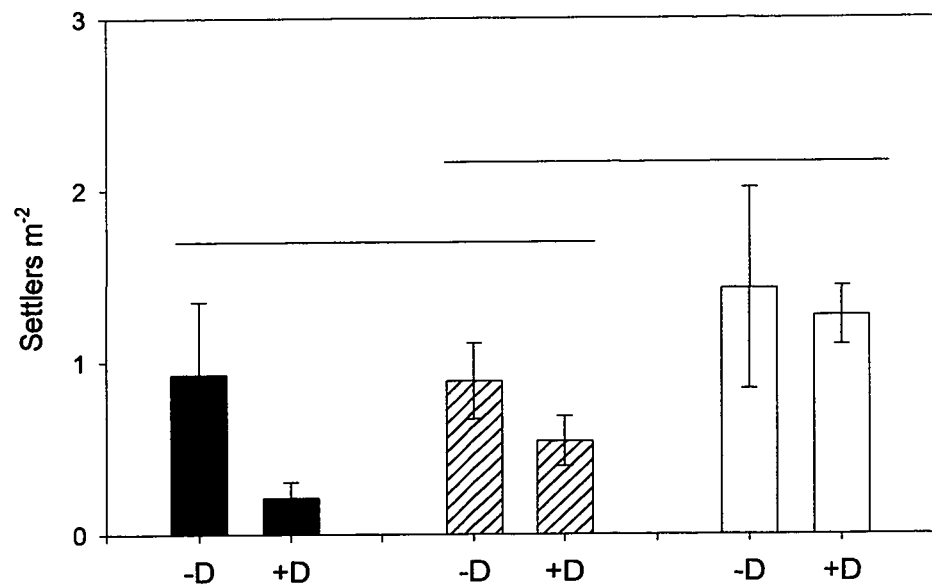


Figure 4.2. Mean total settlement of *S. viride* in the presence and absence of damselfish and at three densities of resident conspecific recruits. Black bars = 0 conspecifics, cross hatched bars = low density of conspecifics ($\sim 0.5 \text{ m}^{-2}$), empty bars = high conspecific density ($\sim 1.0 \text{ m}^{-2}$). Lines indicate treatments that could not be distinguished statistically (Tukey's HSD, $P < 0.05$). Error bars indicate $\pm 1 \text{ SE}$.

but there were also chases between stoplights (Fig. 4.4c). Wrasses (Labridae) and gobies (Gobiidae) were also involved in 1-2 chases per 10 minute observation in all treatments. Several damselfish moved into damselfish exclusion treatments and were involved in a small number of chases, but the number of chases involving damselfishes was greatly reduced. Stoplight 'behavior' was not affected by the density of parrotfish recruits (MANOVA, Pillai Trace = 0.07, $df = 2, 15$, $F = 0.56$, $p = 0.58$), and there was no interaction between terms (MANOVA, Pillai Trace = 0.014, $df = 2, 15$, $F = 0.11$, $p = 0.90$).

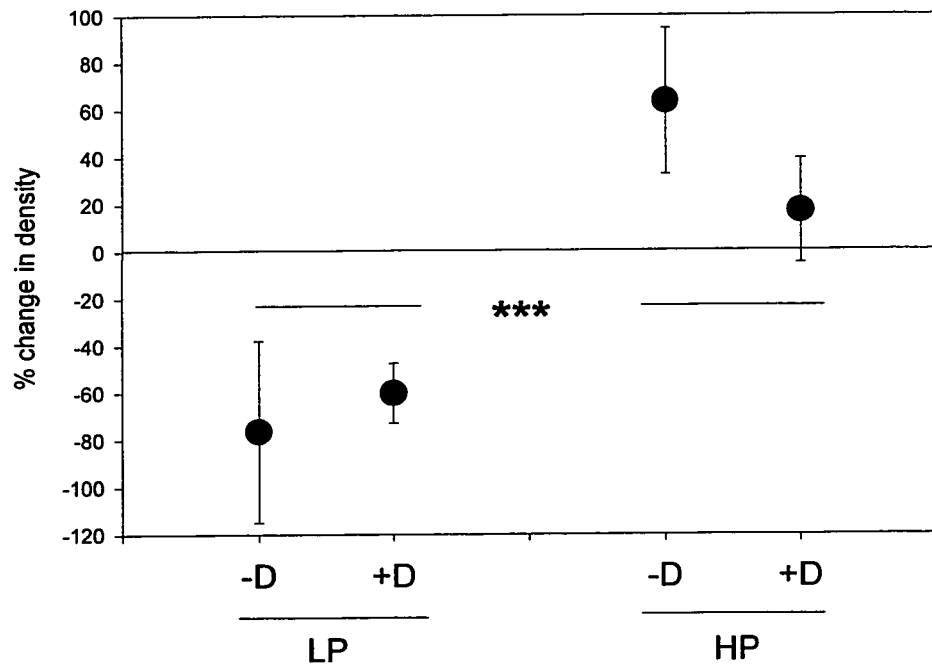


Figure 4.3. Mean percent change (± 1 SE) in density of resident *S. viride* recruits at low (LP) and high (HP) density and in the presence and absence of damselfish. *** indicates $p < 0.001$.

The number of fishes that I was able to re-identify on each patch reef was similar among treatments and after 5 days I was able to re-identify 60-80% of the fishes on all reefs, suggesting that most fishes remained on their original reef for at least a portion of the experiment. After 10 days, I was able to identify only 50% of the tagged fish. This decrease probably resulted from movement of fishes between patch reefs and fading of fin clips.

The total number of fish on all reefs averaged 190.75 when all reefs were pooled (range = 174 - 223, depending on sampling date). Stoplight recruitment was significantly

Table 4.1. Results of repeated measures ANOVA on total recruitment of stoplight parrotfish to *Porites* and *Montastrea* patch reefs in the presence and absence of damselfish. Data were $\ln(x+1)$ transformed prior to analysis.

Source	SS	df	MS	F	p
Between subjects					
Coral	10.349	1	10.349	20.988	<0.001
Damselfish	0.012	1	0.012	0.024	0.878
Coral*Damselfish	2.239	1	2.239	4.540	0.040
ERROR	17.752	36	0.493		
Within Subjects					
Time	0.207	3	0.069	0.933	0.428
Time*Coral	0.977	3	0.326	4.407	0.009
Time*Damselfish	0.266	3	0.089	1.199	0.314
Time*Coral*Damselfish	0.190	3	0.063	0.858	0.465
ERROR	7.978	108	0.074		

higher to *Porites* than to *Montastrea* patch reefs, but this effect was more pronounced on *Porites* patch reefs without damselfish than on *Porites* patch reefs when damselfish were present (Table 4.1, Fig. 4.5). There was also an interaction between coral and census

remained more or less constant on the *Montastrea* reefs after the initial increase.

Examining recruitment by size class revealed that 10 mm, 40 mm, and 50 mm recruits

Table 4.2. Results of two way ANOVA for each size class of fish comparing density of recruits on *Porites* and *Montastrea* patch reefs in the presence and absence of damselfish recruits. Only the results of the coral type are shown since MANOVA did not detect an effect by damselfish nor a significant interaction. Data were $\ln(x+1)$ transformed prior to analysis.

Size	F	p
≤ 10 mm SL	1.694	0.20
≤ 15 mm SL	4.558	0.04
≤ 20 mm SL	50.797	<0.001
≤ 30 mm SL	10.906	0.002
≤ 40 mm SL	0.729	0.399
≤ 50 mm SL	2.976	0.093

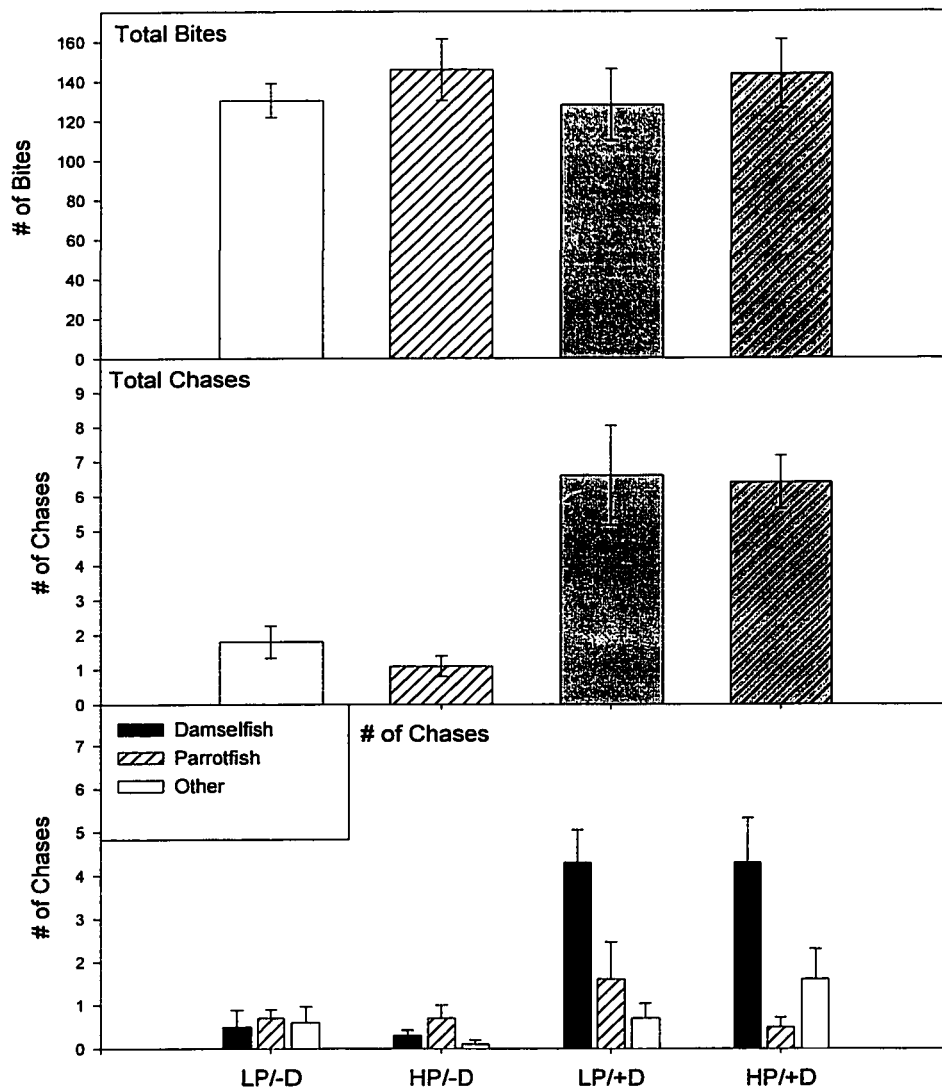


Figure 4.4. Behavior of *S. viride* recruits. HP/LP = high and low parrotfish density; +/-D = damselfish present/excluded.

were more abundant on *Porites* reefs (Fig. 4.6). The density of 15 mm recruits was highest on *Porites* patch reefs when damselfish were excluded, but all other treatments supported similar densities of stoplight recruits of this size class. Slightly larger fishes (20 mm) were more abundant on *Porites* than on *Montastrea* patch reefs, but there was still a trend towards higher recruitment to *Porites* patch reefs without damselfish. For 30 mm recruits, the effect of damselfish disappeared, but local recruitment was still higher to *Porites* reefs than to *Montastrea* ones.

Discussion

There is abundant evidence in the literature that interactions (biotic or abiotic) during settlement between settling individuals and the benthic environment can influence the initial distribution of recruits in the adult habitat, especially at smaller spatial scales. This is true for benthic marine invertebrates (Scheltema 1974; Hadfield 1986; Sunderberg and Kennedy 1993, Morgan et al. 1996) and demersal marine fishes (Sweatman 1985, 1988; Sale et al. 1984a; Wellington 1992; Levin 1993; Tolimieri 1995). Post-settlement processes often reinforce the initial settlement pattern, demonstrating that the choices individuals make during settlement can be important to their future growth and survival (Wellington 1992; Booth 1992, 1995; Tolimieri 1995). For example, Wellington (1992) found that settlement of two damselfish species differed between the fore reef and back reef on the Tague Bay reef. *Stegastes leucostictus* showed higher settlement to the back reef, while *S. variabilis* settled in greater numbers to the fore reef. After settlement, the

on the back reef. Persistence of *S. variabilis* was higher on the fore reef. However, this relationship between choice during settlement and post-settlement processes is not always

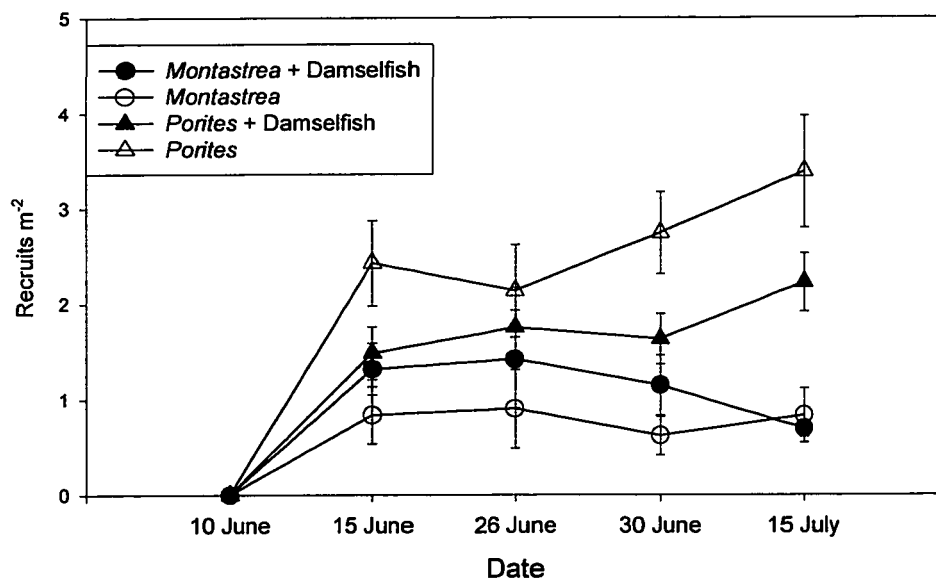


Figure 4.5. Mean change in density of *S. viride* recruits through time. Error bars indicate ± 1 SE.

the case. For example, Levin (1993) showed that recruitment of the cunner, *Tautogolabrus adspersus*, was higher to clumped than to randomly dispersed habitat units. Post-settlement mortality showed the opposite pattern, and within two months there was no difference in settlement to the two habitat types. In the present study, when I found differences that were established at settlement, these differences were reinforced by post-settlement processes as well. However, I also found cases in which the original settlement pattern was significantly altered by post-settlement processes.

emigrated. Ideally, I would have liked to have used more traditional techniques (e.g. Jones 1987a,b; Forrester 1990, 1995; Tolimieri 1995), such as marking resident recruits and then searching the surrounding habitat for any fish that may have moved off of the experimental treatments. I did several pilot experiments testing marking techniques, but I did not find a suitable technique. Although fluorescent dyes made fish easy to identify in the field, most fish marked with fluorescent colors disappeared within several days (Chapter 3, Tolimieri unpublished). Since stoplight recruits are normally somewhat cryptic (pers. obs.), fluorescent dyes probably made them more obvious to predators. In a fin clipping experiment conducted in continuous habitat (Chapter 3), I was able to relocate 11 out of 12 fin clipped fishes over a 10-14 day period. Therefore, it is unlikely that missing fin clipped fish in the present study died from handling. The rapid increase of recruits on cleared reefs suggests that changes in density were due in part to immigration and emigration to and from treatments. Likewise, stoplight densities increased on *Porites* patch reefs when damselfish were excluded. Since this increase cannot have resulted from settlement (I collected all the settlers), the increase must have come from immigration to these treatments.

My data suggest that the distribution and abundance of stoplight parrotfish recruits in relation to the coral substrata was caused by post-settlement processes and not by microhabitat choice during settlement. I draw these conclusions based on the following observations. First, the natural density of stoplight recruits was higher on *Porites* than on *Montastrea*, but settlement did not differ between *Montastrea* and *Porites*

rapid suggesting that recruits immigrated from the surrounding habitat. The arrival of the smallest size class of fish may have been due to both migration and settlement. Finally, differences in recruitment between *Montastrea* and *Porites* patch reefs were not apparent for the smallest size class of recruits (10 mm SL), which would correspond most closely to settlement. Instead, I saw higher recruitment to *Porites* patch reefs by mid-sized recruits (15-30 mm), suggesting that the difference in recruitment to these two substrata developed during the post-settlement stage either by movement of these recruits or by differential mortality, or both. The lack of a difference in density of larger fish probably resulted from the movement patterns of larger fishes. As stoplight recruits become larger, they become more mobile, more active and less cryptic (Chapter 3, pers. obs.) and are probably less dependent on shelter for predator avoidance (at least when these two substrata are concerned). They also were probably moving about over areas that were larger than the individual patch reefs. The low density of these larger fishes on these reefs supports this conclusion.

For coral reef fishes, higher recruitment to some substrata versus others is generally attributed to physical characteristics that provide shelter from predators (Shulman 1984; Hixon and Beets 1989, 1993). In temperate systems, there is evidence that microhabitat use is related to both shelter and food availability (Levin 1994a). My data do not allow me to discriminate between these alternatives. My results indicate that

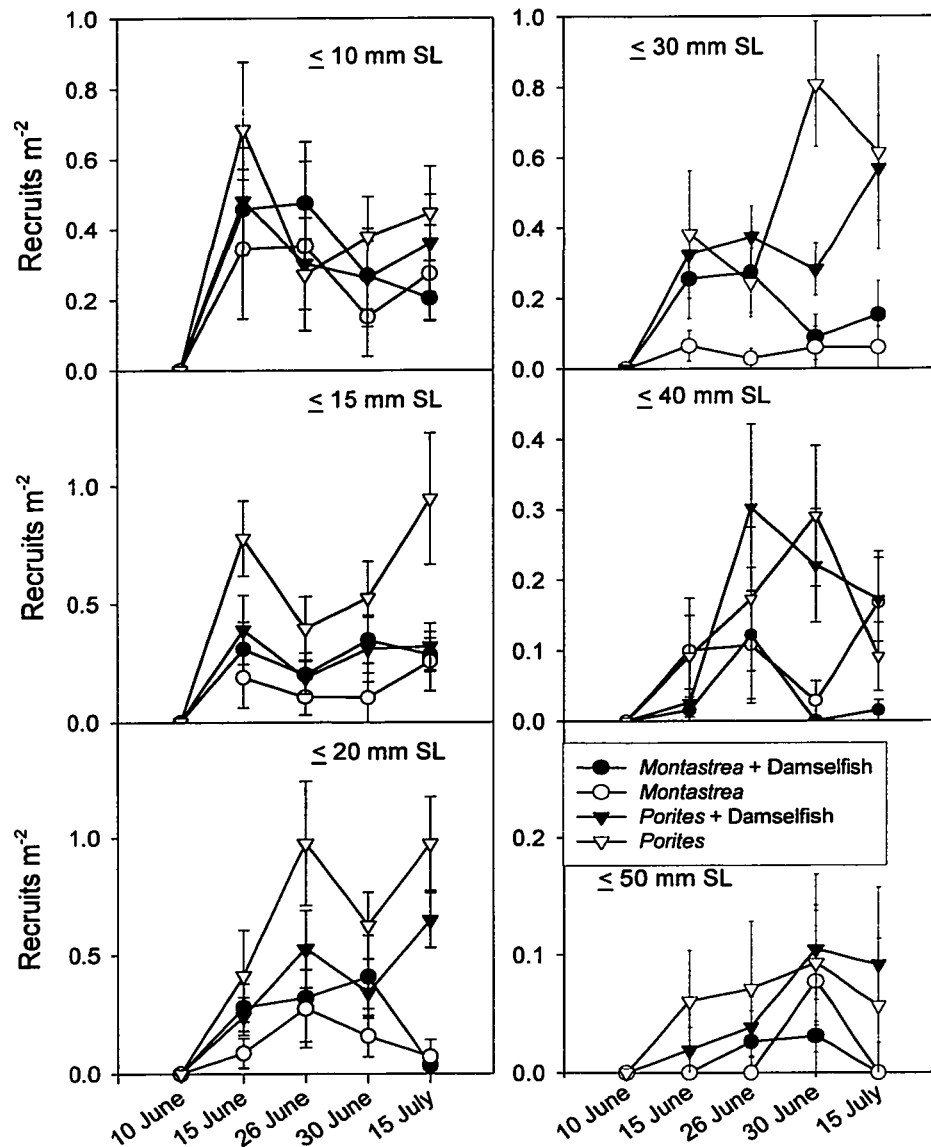


Figure 4.6. Mean change in density of *S. viride* recruits through time separated by size class. Error bars indicate ± 1 SE.

stoplight recruits may be dependent on shelter during the early part of their benthic existence but do not select between *Montastrea* and *Porites* during settlement.

The absence of microhabitat choice during settlement for the stoplight parrotfish is surprising given its prevalence in other species (Sale et al. 1984a; Booth 1992; Levin 1993; Tolimieri 1995; Danilowicz in press) and the higher natural densities and recruitment on *Porites* reefs. For this specific fish species and substratum, the absence of microhabitat choice during settlement may be due to the distribution and growth pattern of the substratum, *Porites*. At the Tague Bay study site, *Porites* forms large mounds 1-3 m in diameter, and whole sections of the reef (100's m²) may consist of monospecific stands (pers. obs.). This pattern (large size, monospecific stands) does not appear to be common at other sites around St. Croix, St. John or Virgin Gorda (pers. obs.) where *Porites* generally produces smaller heads. These smaller patches may be too small to offer increased growth or survival for stoplights relative to other substrata. If this is the case, the benefits of settling to *Porites* may not be widespread enough at large spatial scales and in enough places for stoplight parrotfish to have evolved selection during settlement. This could be tested by examining the relationship between patch size and recruitment.

In contrast to the results concerning substrata, stoplight settlement was higher to reefs containing resident conspecific recruits than to reefs where recruits were absent. Settling with conspecifics appeared to be beneficial during the post-settlement stage because the persistence of stoplight recruits was higher at higher density. Settling individuals may use the presence of members of their own species as cue to indicate a location that has the characteristics that they require. It is not apparent from my data why stoplight persistence was greater in the high density treatments. Originally, I suspected

Table 4.3a. Results of MANOVA on parrotfish behavior on *Porites* and *Montastrea* patch reefs in the presense and absense of damselfishes.

Source	Pillai trace	F	p
Damselfish	0.272	1.805	0.133
Coral	0.083	0.436	0.848
Coral*Damselfish	0.114	0.619	0.713

Table 4.3b. Results of MANOVA on number of chases per 5 min observaton with chases allocated to 4 taxonomic groupings: damselfish, parrotfish, wrasses and blennies.

Source	Pillai trace	F	p
Damselfish	0.501	7.777	<0.001
Coral	0.109	0.949	0.449
Coral*Damselfish	0.116	1.012	0.416

Table 4.3c. Results of ANOVA on number of chases per 5 minute observation period. Results are shown for damselfish effect only since other effects were not significant in the MANOVA

Source	F	p
Damselfish	29.895	<0.001
Wrasses	0.715	0.404
Parrotfish	0.496	0.486
Blennies	1.661	0.206

aggression by damselfish would lower the feeding rate of recruits, and that at higher density the number of chases per individual would decrease as damselfish were forced to defend their territories from more intruders. This speculation is not borne out by the behavioral data, however, as the presence of damselfish did not influence feeding rate. Other researchers have suggested that group size increases predator vigilance (Forrester 1990, 1991) and fishes' ability to find high quality food resources (Clifton 1989, 1990, 1991).

Similar effects of conspecific presence on settlement have been shown in Australian and Hawaiian damselfishes (Sweatman 1985; Jones 1987a,b, Forrester 1988; Booth 1992). For these species, growth can be reduced by intraspecific competition (Jones 1987a,b, 1988a; Forrester 1990, Booth 1995), but survivorship may be increased in larger groups (Booth 1995) or in the presence of adults (Forrester 1990)-presumably because larger groups are better at spotting predators. Clifton (1989, 1990, 1991) found different results in *Scarus iserti*, a Caribbean parrotfish in which groups of unrelated female fishes are territorial. Larger groups were better able to defend territories and located high quality food more quickly than small groups. This increased the growth rate of the largest fish in the group, which would eventually change sex into a terminal phase male and vacate the territory.

I find it somewhat surprising that damselfish did not significantly affect parrotfish settlement. Damselfish are highly aggressive and defend territories against egg predators and potential food competitors (Thresher 1976; Itzkowitz 1990). Resident damselfish are

Robertson (1996) demonstrated that three-spot damselfish, *Stegastes planifrons*, excludes two other damselfish from its preferred habitat. In the present study, damselfish frequently chased stoplight recruits. There were non-significant trends towards lower settlement in the presence of damselfish, and the low power of my experiment to detect an effect may explain the lack of a difference. Damselfish did affect parrotfish recruitment, which was significantly higher to *Porites* patches without damselfish than to other treatments. While these interactions may explain the higher recruitment of stoplights in the absence of damselfish within the *Porites* treatment, they do not explain differences in recruitment between the coral types. These interactions may have affected growth, but I find that unlikely since feeding rates did not differ between the presence or absence of damselfish. Damselfish may have excluded stoplight recruits from higher quality food resources, but I cannot address that question here.

In conclusion, the small scale recruitment of stoplight parrotfish appears to be influenced by several factors both during and after settlement. Stoplights showed contagious settlement but did not appear to select between two substrata during settlement. Conspecific density affected the local persistence of stoplight recruits with higher persistence at higher density, and coral type affected recruitment during the post-settlement stage. These results show that both pre- and post-settlement processes are important in determining recruitment patterns for the stoplight parrotfish. They also demonstrate that post-settlement processes can alter the initial pattern of settlement and disrupt the relationship between settlement and recruitment.

DISTRIBUTION AND ABUNDANCE OF CORAL REEF FISHES AT TWO SPATIAL SCALES

Abstract

Coral reefs are patchy environments across several spatial scales, and an important question for ecologists is whether the processes that influence the distribution of organisms within patches also influence the distribution and abundance of organisms among patches. I examined the relationship between microhabitat use within sites and the distribution and abundance among sites for the adults of 11 species of Caribbean reef fishes (6 pomacentrids and 5 scarids). Within sites all species associated with one or more substrata more than would be expected at random. Not all species associated with the same substrata. The abundance of these 11 species varied greatly among 13 sites located along the northern shore of St. Croix, U.S.V.I.. Microhabitat use within sites explained approximately 30--35% of the variation in abundance among these 13 sites for three of the six damselfish species (*Stegastes planifrons*, *S. partitus*, and *Microspathodon chrysurus*). For a fourth damselfish, *S. dorsopunicans*, microhabitat use explained approximately 85% of the variation in its abundance among sites. Only one parrotfish (*Scarus iserti*) showed any relationship between microhabitat use and the distribution of adult fishes among sites with approximately 50% of the variation in its abundance explained by a combination of microhabitat and distance from the eastern tip of the

may play a part in determining the distribution and abundance of marine fishes at larger spatial scales for some species. They also suggest that the importance of microhabitat use to the distribution of a species may have a taxonomic basis.

Introduction

Marine ecosystems are patchy across several spatial scales. As a result, populations of benthic or demersal marine organisms exist as a series of local populations in an open system where dispersal among patches is essential to the persistence of each local population and the metapopulation as a whole (Hanski and Gilpin 1991). These populations may or may not be metapopulations in the classic sense (Hanski and Gilpin 1991; Hanski et al. 1995; Man et al. 1995). Nevertheless, they do function under similar considerations concerning dispersal among patches and the persistence of populations within patches. Increasingly, however, metapopulation theory has focused on the importance of within patch dynamics (e.g., patch quality) to the distribution and abundance of the overall metapopulation. An important question for ecologists is whether the processes that influence the distribution of organisms within patches also influence the distribution and abundance of organisms among patches.

For most marine organisms, dispersal among patches (i.e., reefs) is undertaken by pelagic larvae, which leave the local patch and eventually settle to another one. However, once an individual has arrived in a local patch, it will normally spend the remainder of its

the larval stage can last from 9-100 days (depending on the species) allowing for dispersal over large distances (Leis 1991). Adults are often site attached and territorial, may have very limited home ranges (Sale 1971, 1978, 1991a; Clifton 1989, 1990, 1991), and usually remain within one reef their entire life (but see Robertson 1988a). Because of the patchiness of the coral reef environment and the complex life-cycle of reef fishes, the population dynamics of fishes on coral reefs can be influenced across several spatial scales and by processes operating during the pelagic or demersal stages of the life-cycle.

Processes that influence larval supply to patches, such as oceanic currents (Haury et al. 1978; Victor 1986; Williams et al. 1984; Cowen and Castro 1994), internal waves or tidal patterns (Shanks 1983; Kingsford and Choat 1986; Shanks and Wright 1987), eddies (Leis 1986; Shultz and Cowen 1994) and stochastic weather events (Shenker 1993; Sponaugle and Cowen 1994) function at scales larger than the local patch or reef. These processes determine the supply of larvae to patches of habitat. Larval supply can determine the amount of settlement to a reef or habitat (Victor 1984, 1986; Gaines et al. 1985; Milicich et al. 1992; Meekan et al. 1993), and settlement patterns usually correlate with recruitment patterns (Victor 1984, 1986; Williams et al 1994; Tolimieri 1995; Levin 1996). Recruitment, in turn, may directly limit adult population size (Williams 1980; Doherty 1983; Doherty and Fowler 1994a,b). Therefore, these pre-settlement processes can determine the distribution of fishes among reefs by controlling the arrival of larvae to reefs.

Demersal processes like microhabitat use (Eckert 1985; Tolimieri 1995; Caselle

1987a,b, 1988, 1991; Forrester 1995; Clarke 1992, 1996; Robertson 1995, 1996), and predation (Hixon and Beets 1989, 1993; Hixon 1991; Caley 1995; Carr and Hixon 1995) function within patches and influence local population and community dynamics. Do the factors regulating demersal processes (local population dynamics) that affect the distribution and abundance of fishes within sites also influence their distribution and abundance among sites? Alternatively, population and community dynamics at the metapopulation scale may be controlled by non-benthic processes that determine the rate of larval supply to a reef. These questions have obvious importance if we intend to understand and potentially manage reef ecosystems.

Microhabitat use affects the distribution of fish within reefs or locations on both coral and temperate rocky reefs (Sale et al. 1984a; Ebersole 1985; Carr 1991, 1994; Levin 1991, 1993, 1994b; Booth 1992; Macpherson 1994; Tolimieri 1995, in press; Garcia-Rubies and Macpherson 1995; Green 1996; Caselle and Warner 1996; Levin and Hay 1996). Attributes of the reef have also been shown to correlate with diversity and abundance of fishes among reefs (Nagelkerken 1977; Luckhurst and Luckhurst 1978; Warner and Hoffman 1980; Thresher 1983; Bell and Galzin 1984; Tolimieri in press). Many of these studies, however, have looked at only one spatial scale, and few studies have addressed the influence of habitat or microhabitat use on adult abundance at several spatial scales. Moreover, the majority of studies on coral reef fishes have examined the effects of various processes on recruitment or the demography of juvenile fishes and have ignored adult fishes (but see Forrester 1995; Robertson 1996).

reef fishes from two families (Pomacentridae and Scaridae) at two spatial scales. My primary goal was to determine whether microhabitat use explained the distribution and abundance of adult fishes among patches. I begin by quantifying microhabitat use by individual fish in two different habitats on the same reef. I then determine whether the microhabitat characteristics that were important in describing the distribution of fishes within sites are important in explaining variation in abundance among sites.

Methods

Within-site microhabitat use

I quantified small spatial scale microhabitat use by the adults of six damselfish (Pomacentridae) and five parrotfish (Scaridae) species on the fore reef slope and back reef of the Tague Bay reef, St. Croix, USVI (17°45'N, 64°42'W, Fig 5.1). The Tague Bay reef is a barrier bank type reef comprised primarily of dead *Acropora palmata*, live and dead *Porites porites*, and *Montastrea annularis*. The reef reaches its base at approximately 10-15 meters where it begins to break up into patch reefs, individual coral heads, and sand. Damselfish species included the three-spot, *Stegastes planifrons*; dusky, *S. dorsopunicans*; longfin, *S. diencaeus*; bicolor, *S. partitus*; the beaugregory, *S. leucostictus*, and the yellowtail damselfish, *Microspathodon chrysurus*. Parrotfish

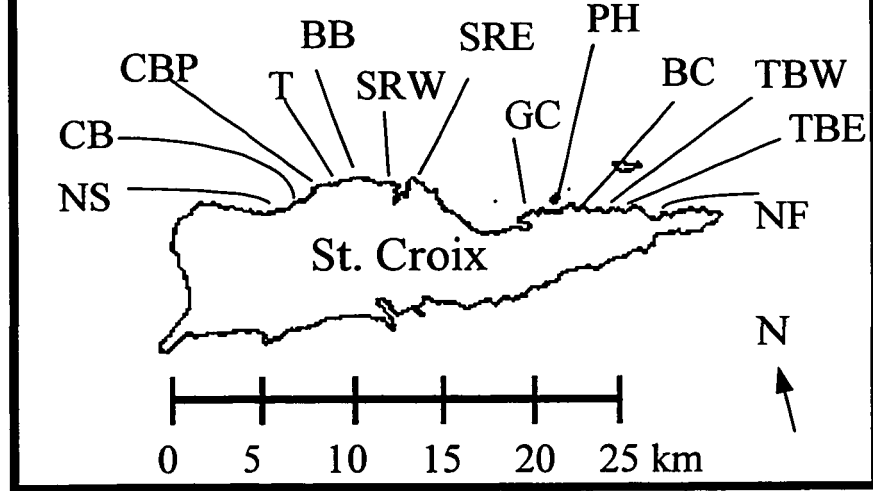


Figure 5.1. Location of the study sites. NF = Nick's Folly; TBE & TBW = Tague Bay east and west; BC = Boat Cut; PH = Pink Hotel; GC = Green Cay; SRE & SRW = Salt River east and west walls; BB = Baron's Bluff; T = Mill Tower; CBP = Cane Bay Point; CB = Cane Bay; NS = North Star

species were: the redband, *Sparisoma aurofrenatum*; stoplight, *S. viride*; queen, *Scarus vetula*; redfin (a.k.a. yellow tail), *S. rubripinne*, and striped parrotfish, *S. iserti*.

I used different methods to quantify microhabitat use by damselfishes and parrotfishes based on the degree to which the two families moved around on the reef. Damselfishes (*Chromis spp.* aside) are aggressive, territorial and site attached at very small spatial scales, and occupy territories 1.0-2.0 m² (Sale 1971; Thresher 1976; Kaufman 1977). Adult parrotfishes tend to be much more mobile and move about over areas closer to 20-100 m² in size (pers. obs.). An important question for ecologists to consider is whether the processes that influence the distribution of organisms within patches also influence the distribution and abundance of organisms among patches. In both cases, however, I compare the microhabitat characteristics of areas occupied by fish to the microhabitat characteristics available at random.

substrata in areas occupied by individual fish to the substrata that was available at random about the reef. To sample quadrats occupied by fish, a diver set out a 30 meter transect line parallel to the reef slope at 5-10 meters depth on the fore reef and 2-5 meters depth on the back reef. The diver then swam along this transect and searched for damselfishes located within one meter of either side of the transect line. When a fish was sighted, the diver centered the quadrat on the location where the fish was first seen and recorded the substratum present under 49 points within the quadrat (a 7 x 7 grid). To sample null (random) quadrats, a diver swam along a transect line and placed the quadrat at pre-determined, random distances along the transect. Null quadrats were sampled along transects which had already been sampled for fishes, and along separate transects in the same general area. Not all fish transects were sampled for null quadrats.

To quantify microhabitat use by parrotfishes, I compared the substrata used during five minute focal animal observations to the microhabitat characteristics recorded along 15 meter transects. During focal animal observations, I followed an individual fish for five minutes and recorded the substratum the fish was over every five seconds (60 observations). Transects were laid out parallel to the reef face in the same general area. I then recorded the substratum present under every 25 cm along the transect (60 points). During fish observations, the diver was careful to maintain a distance that did not disturb the subject. Any observations during which the observer felt that he had disturbed the fish were discarded. One species in particular, *S. rubripinne*, proved very sensitive to

species. The substratum categories that I recorded were the same as for the damselfishes.

For both quadrats and transects, I recorded the percent cover of the following nine substratum categories: ‘*Porites*’, ‘*Porites* rubble’, ‘*Montastrea*’, ‘*Montastrea* rubble’, ‘*Acropora* rubble’, ‘live coral’, ‘boulder rubble’, and ‘pavement’. The category ‘*Porites*’ included living *Porites porites*, a digitate coral, while the category ‘*Porites* rubble’ included dead coral that could still be easily identified as *P. porites*. ‘*Montastrea*’ included living *Montastrea annularis*, a common massive coral, while ‘*Montastrea* rubble’ refers to dead *M. annularis*. Likewise, ‘*Acropora* rubble’ refers to dead *Acropora palmata*, a large branching coral. The group ‘live coral’ included all live coral except *M. annularis* and *P. porites*. The category ‘boulder rubble’ consisted of all unidentifiable dead coral. ‘Pavement’ referred to flat, eroded coralline rock.

I used multivariate analysis of variance (MANOVA) to determine whether microhabitat use by a species differed from what would be expected at random. Analyses were conducted separately for damselfishes and parrotfishes, although all species within a family were included in the same analysis. In the analyses, species are considered the independent variable and the microhabitat characteristics of the quadrats or transects/observations are the dependent variables. I used individual contrasts to compare each species to the null data. For the contrasts, p-values were Bonferroni adjusted to protect the overall experimental α . Prior to analysis, I arcsine transformed all data to control for heteroscedacity and to normalize the data (Zar 1984; Tabachnick and Fidell 1989). I also examined the canonical loadings and plotted canonical variates from the

differences (1) between quadrats occupied by fish and null quadrats for the damselfishes, and (2) between substrata over which fish spent time and null transects for the parrotfishes.

Relationship between within site microhabitat use and among site abundance

To determine whether within site microhabitat use predicted the distribution and abundance of fish at a larger spatial scale, I examined the relationship between microhabitat characteristics and fish abundance among 13 sites spanning approximately 25 km along the northern coast of St. Croix (Fig 5.1). Sites were chosen primarily based on accessibility and generally included areas $>2000 \text{ m}^2$ in extent. All sampling was conducted at 6-10 meters depth, and I used 30 x 2 meter transects to quantify the abundance of fishes at each site. A diver laid out a 30 meter transect line and then waited several minutes before beginning to swim along the transect and recording all fish within one meter of either side of the line. The diver also recorded the substratum present under every 25 cm (120 points). These data were recorded in three passes along the transect. On the first pass, the diver recorded the more mobile species (parrotfishes). On the second pass, the diver counted the damselfishes, and on the third pass the diver quantified the substratum. I recorded the same substratum groupings as in the within sites analysis, and 16 transects were done at each site.

I used forward step-wise regressions (minimum tolerance = 0.01, α to include in model = 0.15) to examine the relationships between fish abundance and microhabitat

dependent variable and the mean proportional cover of the substrata as the independent variables. Each species was analyzed separately. I placed two *a priori* limitations on the substrata included in the model: (1) prior to the analysis, I included only those substrata that influenced the species distribution within a patch, and (2) once the regression was run, I removed substrata with ‘unexpected correlations’ from the model and re-ran the analysis. An ‘unexpected correlation’ occurred when a species’ abundance was correlated with a substratum in the opposite direction from which I expected based on the small scale analyses. For example, if *S. planifrons* associated with *Montastrea* within sites, I expected *S. planifrons* abundance to be positively correlated with *Montastrea* among sites. I would consider a negative correlation between *S. planifrons* and *Montastrea* cover to be an ‘unexpected correlation’. If such a situation occurred, I would remove *Montastrea* from the model and re-run the analysis. I added these limitations for two reasons. First, my main question was whether small scale microhabitat use predicted the abundance of a species among locations. Therefore, a substratum that a species neither associated with nor avoided at a small spatial scale would not provide any information relevant to the question. Likewise, if I found an ‘unexpected correlation’, I could conclude that large scale abundance was not influenced by small spatial scale microhabitat use. Second, multiple regression requires large data sets to provide robust results (Tabachnick and Fidell 1989). As the number of independent variables increases in relation to the number of replicates, the probability of chance correlations become more common (Tabachnick and Fidell 1989). Therefore, I wanted to eliminate any

In the results section, however, I present both the results from the first run through of the step-wise regressions and the final model with unexpected correlations removed so that the reader may evaluate both. Finally, I also included a new variable: distance from the eastern end of St. Croix (KM) to account for the spatial location of the sites. Therefore, each step-wise regression began with 4--5 predictor variables, and generally only one substratum was included in the final model. All analyses were done using the SYSTAT statistical package.

Results

Microhabitat use within sites

Microhabitat characteristics were similar, though not exactly the same, on the fore reef and back reef habitats at the Tague Bay reef, although live *Porites* was more abundant on the fore reef at the sites sampled (Fig 5.2). Multivariate analysis of variance (MANOVA) indicated that microhabitat characteristics differed significantly among the null quadrats and the quadrats occupied by the five species of damselfish on the fore reef (Pillai trace = 0.555, df = 30, 650, $F = 3.457$, $p < 0.001$) and on the back reef (Pillai trace = 1.105, df = 36, 554, $F = 6.064$, $p < 0.001$). For the fore reef, contrasts indicated that *S. planifrons*, *S. partitus* and *M. chrysurus* associated with some substrata more than would be expected than at random (Table 5.1). However, *S. diencaeus* and *S. dorsopunicans* were distributed randomly with respect to substratum characteristics. Examination of

associated with *Montastrea*, *Porites* and *Acropora* rubble more than would be expected

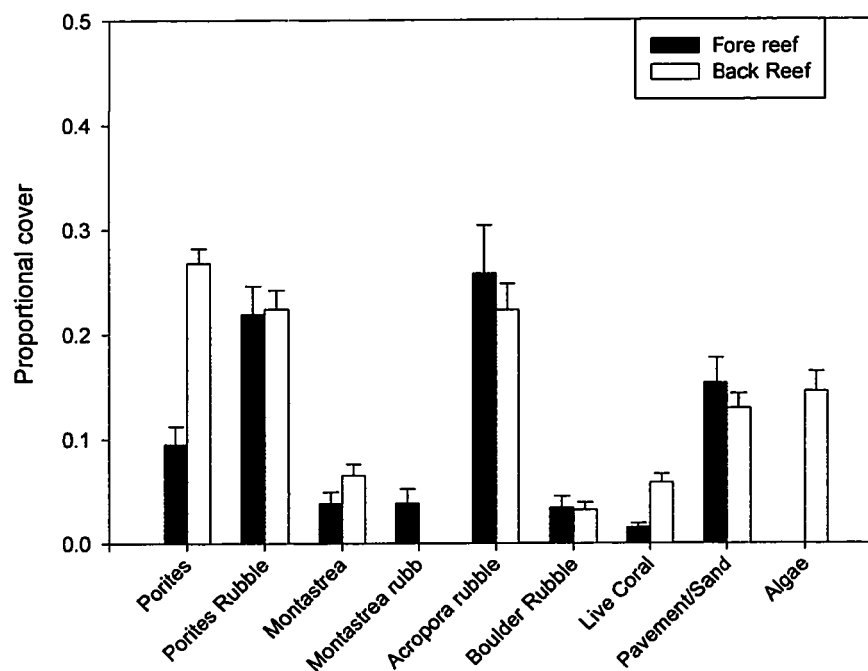


Figure 5.2. Mean proportional cover of 9 substrata on the fore reef and back reef at Tague Bay. Error bars indicate ± 1 SE.

at random, and avoided *Porites* rubble (Fig 5.3, Table 5.2). *S. partitus* associated with *Montastrea* and *Porites* rubble more than would be expected at random. Finally, *Acropora* rubble was more abundant in the quadrats occupied by *M. chrysurus* damselfish than in null quadrats.

On the back reef, *S. planifrons* associated with *Acropora* rubble and *Porites* rubble more than would be expected at random (Fig 5.4, Table 5.3). *S. diencaeus* and *S.*

damselfish were very rare, and I did not sample their microhabitat use on the back reef.

However, the beaugregory damselfish, *S. leucostictus*, a damselfish that is common in this back reef habitat, occupied areas with more *Porites* rubble than the null quadrats.

Table 5.1. Results of contrasts comparing microhabitat use by individual species to microhabitats at null sites for parrotfish and damselfish on the fore reef and back reef. n indicates # of quadrats done per species.

Species	Fore reef	n	Back reef	n
Damselfish				
<i>Stegastes planifrons</i>	<0.001	26	<0.001	24
<i>S. partitus</i>	0.014	32		0
<i>S. diencaeus</i>	0.081	21	<0.001	33
<i>S. dorsoponicans</i>	0.207	29	<0.001	33
<i>S. leucostictus</i>		0	<0.001	25
<i>Microspathodon chrysurus</i>	0.007	25		0
Null		40		38
Parrotfish				
<i>Sparisoma viride</i>	<0.001	26	<0.001	27
<i>S. aurofrenatum</i>	<0.001	25	<0.001	19
<i>S. rubripinne</i>	<0.001	6	<0.001	6
<i>Scarus vetula</i>	<0.001	25	<0.001	19
<i>S. iserti</i>	<0.001	25	<0.001	24
Null	32	32		

Parrotfishes did not associate randomly with the substrata on the fore reef

(MANOVA, Pillai trace = 1.739, df = 45, 645, F = 7.645, p < 0.001) nor on the back reef

(MANOVA, Pillai trace = 1.083, df = 45, 585, F = 3.594, p < 0.001). Contrasts showed

associated with some substratum more than would be expected if the fish used the substratum at random (Table 5.1). Examination of canonical loadings and plotting of the first two canonical variates showed that all parrotfish species spent more time over

Table 5.2. Canonical loadings for discriminant function analysis of small scale habitat use by Caribbean damselfish and parrotfish on the fore reef at Tague Bay. Data for adult damselfish and recruits come from 1.0 m² quadrats. Data for adult parrot fish are based on 5 minute observations and 15 m transects. NS = non significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Substrata	Factor 1	Factor 2	Factor 3
Adult damselfish			
<i>Porites</i>	0.232	-0.772	0.063
<i>Porites</i> rubble	0.888	0.035	-0.190
<i>Montastrea</i>	-0.259	-0.460	0.380
<i>Montastrea</i> rubble	-0.209	-0.348	0.605
<i>Acropora</i> rubble	-0.558	0.457	-0.212
Boulder rubble	-0.324	-0.019	0.450
Canonical correlation	0.522***	0.405***	0.275 ^{NS}
Adult parrotfish			
<i>Porites</i>	-0.803	-0.467	0.043
<i>Porites</i> rubble	0.281	-0.572	0.274
<i>Montastrea</i>	-0.267	0.026	-0.003
<i>Montastrea</i> rubble	0.049	0.161	-0.087
<i>Acropora</i> rubble	0.094	0.702	0.025
Boulder rubble	0.102	-0.226	-0.170
Live coral	-0.290	-0.052	0.694
Pavement/Sand	-0.452	0.202	0.198
Algae	0.023	-0.003	0.118
Canonical correlation	0.875***	0.752***	0.426***

Porites rubble than would be expected at random (Fig 5.5, Table 5.2). In addition, *S. vetula* associated with *Acropora* rubble, and *S. iserti* utilized areas with live *Porites*.

the null expectations (Fig 5.6, Table 5.3). *S. aurofrenatum* used more pavement than was available at random. Other species tended to spend time over areas with *Acropora rubble*, while *S. iserti* also tended to occupy areas with pavement or sand as well.

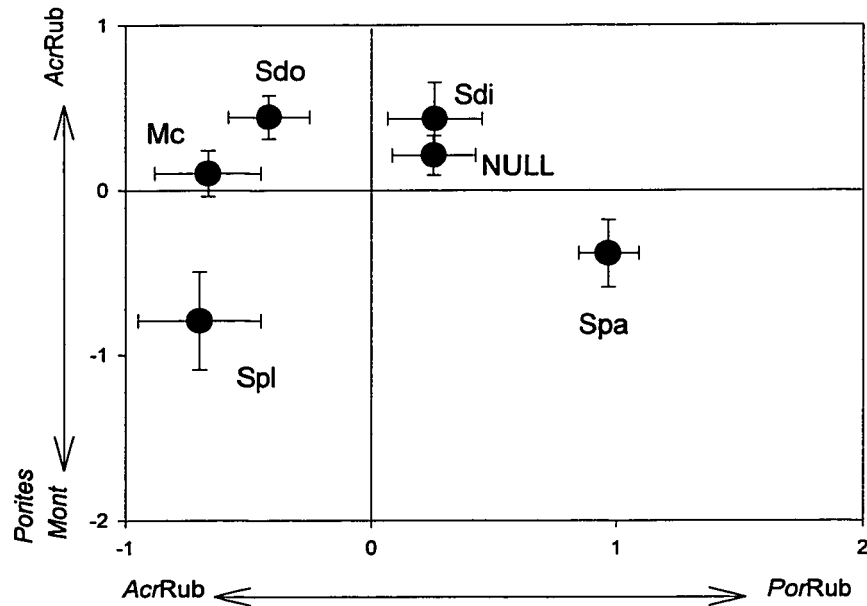


Figure 5.3. Plot of the first (x-axis) and second (y-axis) canonical variates describing damselfish microhabitat use on the fore reef. Mc = *Microspathodon chrysurus*, Sdo = *Stegastes dorsopunicans*, Sdi = *S. diencaeus*, Spl = *S. planifrons*, Spa = *S. partitus*. Mont = *Montastrea*, AcrRub = *Acropora* rubble, PorRub = *Porites* rubble. Bars indicate ± 1 SE.

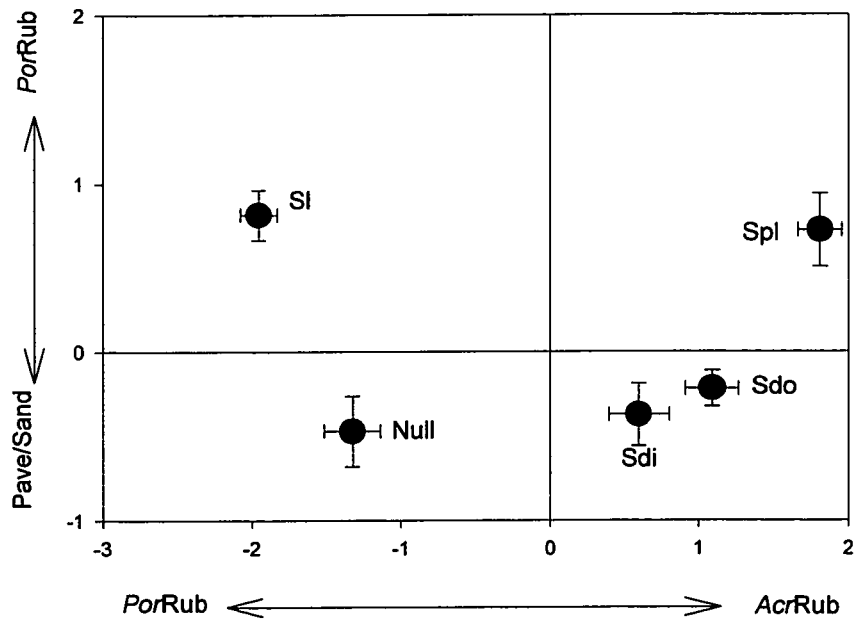


Figure 5.4. Plot of the first (x-axis) and second (y-axis) canonical variates describing damselfish microhabitat use on the back reef. Sdo = *Stegastes dorsopunicans*, Sdi = *S. diencaeus*, Spl = *S. planifrons*, Slu = *S. leucostictus*. Mont = *Montastrea*, AcrRub = *Acropora* rubble, PorRub = *Porites* rubble. Bars indicate ± 1 SE.

Table 5.3. Canonical loadings for discriminant function analysis of small scale habitat use by Caribbean damselfish and parrotfish on the back reef at Tague Bay. Data for adult damselfish and recruits come from 1.0 m² quadrats. Data for adult parrot fish are based on 5 minute observations and 15 m transects. NS = non significant, * p < 0.05, ** p < 0.01, *** p < 0.001.

Substrata	Factor 1	Factor 2	Factor 3
Adult damselfish			
<i>Porites</i>	-0.176	-0.364	-0.364
<i>Porites</i> rubble	-0.648	0.654	0.240
<i>Montastrea</i>	0.042	-0.309	-0.420
<i>Montastrea</i> rubble	0.220	0.118	-0.656
<i>Acropora</i> rubble	0.461	-0.343	0.668
Boulder rubble	-0.054	-0.021	0.037
Pavement/Sand	-0.179	-0.530	-0.162
Algae	-0.205	0.067	0.057
Live Coral	0.253	0.061	-0.133
Canonical correlation	0.814***	0.478***	0.360**
Adult parrotfish			
<i>Porites</i>	0.164	0.488	0.033
<i>Porites</i> rubble	0.564	0.296	-0.330
<i>Montastrea</i>	0.213	0.001	0.752
<i>Montastrea</i> rubble	0.030	0.052	-0.043
<i>Acropora</i> rubble	-0.767	0.319	-0.064
Boulder rubble	-0.041	-0.316	0.061
Live coral	0.059	0.268	0.016
Pavement/Sand	0.449	-0.623	0.017
Algae	0.619	-0.116	0.256
Canonical correlation	0.724***	0.517***	0.434*

Microhabitat characteristics and variation in abundance among sites

I eliminated three of the original eleven species from the large spatial scale analysis because they were not abundant enough among sites to warrant statistical analysis (Fig 5.7). Microhabitat characteristics varied among sites but only the frequency

correlated with distance from the eastern tip of the island. The central sites tended to have higher percent cover of pavement or sand than other sites.

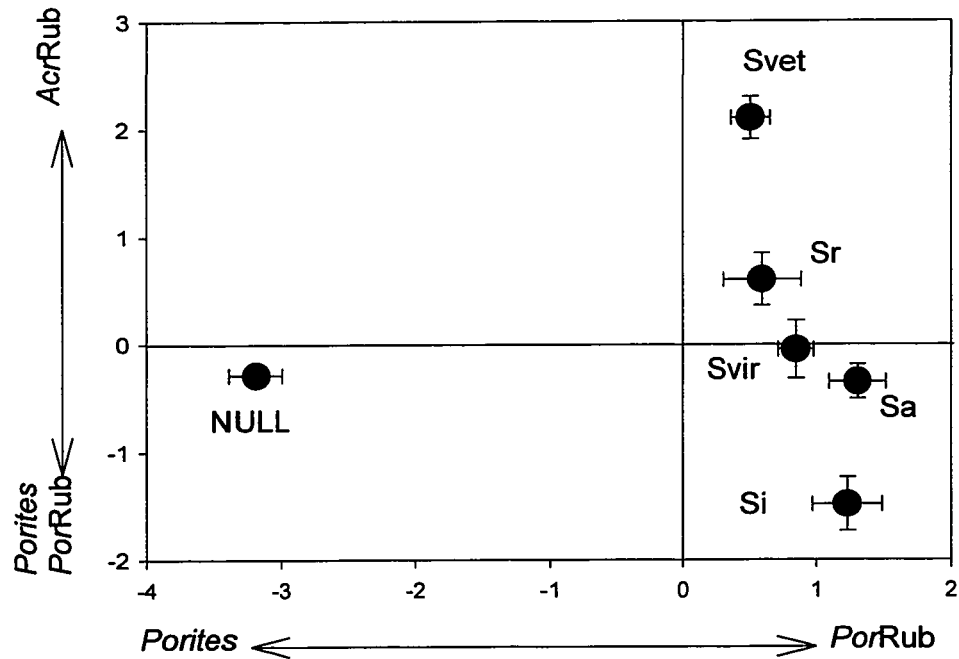


Figure 5.5. Plot of the first (x-axis) and second (y-axis) canonical variates describing parrotfish microhabitat use on the fore reef. Svet = *Scarus vetula*, Svir = *Sparisoma viride*, Sa = *S. aurofrenatum*, Si = *S. iserti*, Sr = *S. rubripinne*. AcrRub = *Acropora* rubble, PorRub = *Porites* rubble. Error bars indicate + 1SE.

Four of the five damselfish showed correlations between the substrata important at small spatial scales and variation in abundance among sites (Table 5.4). Forty percent of the variation in abundance of *S. partitus* among sites was explained by the percent cover of *Montastrea* (Fig 5.8a). For *S. planifrons*, 96% of the variation in adult

Table 5.4. Results of stepwise regression analysis to determine whether small scale habitat use predicts large scale abundance of adults among 10 sites. Data used in the analysis are the mean abundance of each species and substratum along 10 transects at each site. The substrata included in the initial model are based on substrata important in combined discriminant function analysis. Regressions were done only for those species that demonstrated non-random habitat use at a small spatial scale. *Por* = *Porites*, *PorRub* = *Porites* rubble, *Mont* = *Montastrea*, *MontRub* = *Montastrea* rubble, *Acr* = *Acropora* rubble. Bold face type indicates substrata that were correlated with fish abundance in the direction (+/-) predicted by the small spatial scale study. NS = non significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Species	Substrata included in analysis	Substrata included in model	coefficient	r^2
Damselfish				
<i>Stegastes planifrons</i>	<i>Por</i> , <i>PorRub</i> , <i>Mont</i> , <i>Acr</i> , KM	<i>Por</i> <i>PorRub</i> <i>Mont</i> KM	-2.08 14.44 24.84 0.08	0.96***
<i>Stegastes partitus</i>	<i>Por</i> , <i>PorRub</i> , <i>Mont</i> <i>Acr</i> , KM	<i>Mont</i>	31.78	0.40*
<i>Stegastes dorsoponicans</i>	<i>Acr</i> , P/S, KM	<i>Acr</i> KM	36.52 -0.21	0.90***
<i>Stegastes diencaeus</i>	<i>Acr</i> , P/S, KM	<i>Acr</i>	7.60	0.14 ^{NS}
<i>Microspathodon chrysurus</i>	<i>Por</i> , <i>PorRub</i> , <i>Mont</i> ,	<i>Por</i> <i>PorRub</i> <i>Acr</i> <i>Mont</i>	0.11 17.07 5.82 2.12	0.99***
Parrotfish				
<i>Sparisoma viride</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , KM	<i>Por</i> <i>Acr</i>	3.32 2.05	0.85***
<i>Sparisoma aurofrenatum</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , KM	no model		
<i>Scarus iserti</i>	<i>Por</i> , <i>PorRub</i> , <i>Acr</i> , KM	<i>Por</i> <i>PorRub</i> KM	9.24 -11.76 -0.06	0.99***

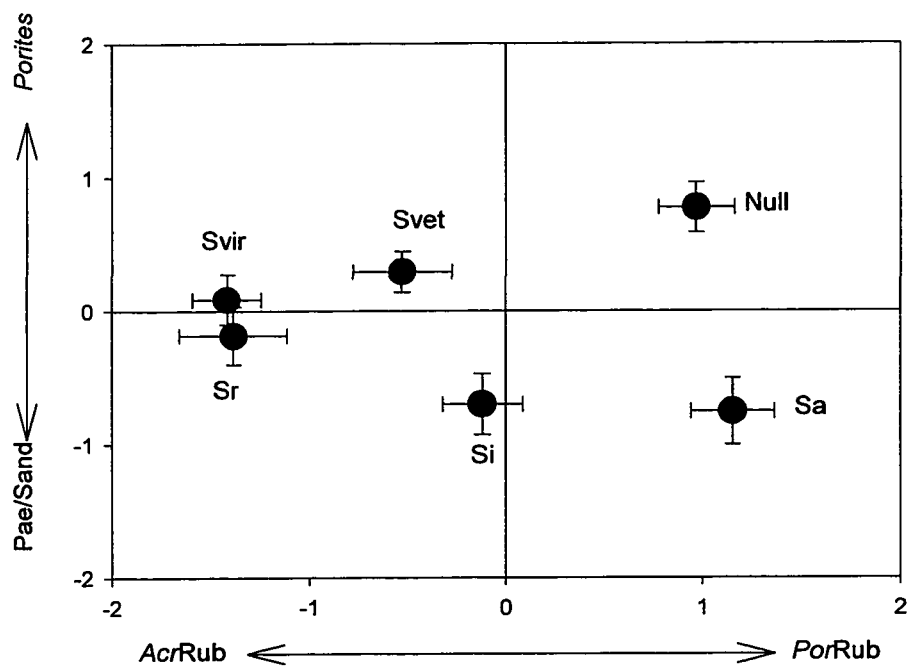


Figure 5.6. Plot of the first (x-axis) and second (y-axis) canonical variates describing parrotfish microhabitat use on the back reef. Svet = *Scarus vetula*, Svir = *Sparisoma viride*, Sa = *S. aurofrenatum*, Si = *S. iserti*. AcrRub = *Acropora* rubble, PorRub = *Porites* rubble, Pave/Sand = pavement and sand. Error bars indicate ± 1 SE.

abundance among sites was explained by microhabitat characteristics, but two of the four substrata in the model showed unexpected correlations. If these two substrata are excluded, the percent cover of *Montastrea* (+) and the distance from the eastern tip of St. Croix (-) explained 49% of the variation in *S. planifrons* abundance ($r^2 = 0.493$, $p = 0.034$). *Montastrea* by itself explained 35% of the distribution of *S. planifrons* among

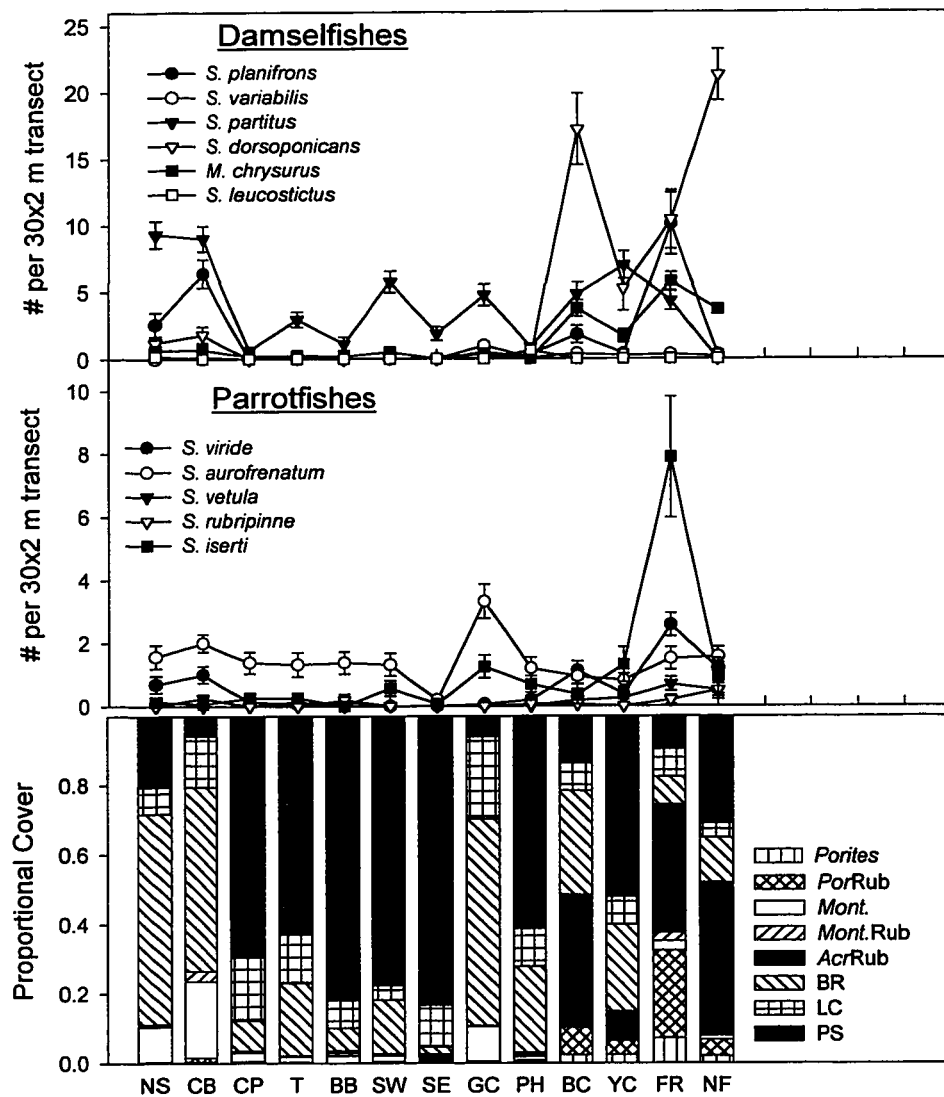


Figure 5.7. Mean abundance of (a) damselfish and (b) parrotfish at 13 sites around St. Croix, and (c) cover of 8 microhabitat characteristics at the same sites. Error bars indicate $\pm 1SE$ PorRub = *Porites* rubble, Mont = *Montastrea*, MontRub = *Montastrea* rubble, AcrRub = *Acropora* rubble, BR = boulder rubble, LC = other live coral, PS = pavement and sand. Sites are listed on the x-axis. Refer to Fig. 5.1 for location of sites.

sites ($r^2 = 0.346$, $p = 0.035$, Fig 8b). Similarly, 99% of the variation in abundance among sites of the *M. chrysurus* damselfish was explained by microhabitat characteristics, but

correlations'. If these substrata are excluded, *Acropora* rubble is correlated with the abundance of *M. chrysurus* damselfish and, this relationship explains 32% of the variation ($r^2 = 0.322$, $p = 0.043$, Fig 5.8c). *S. dorsopunicans* showed the strongest correlations between habitat use and abundance. The percent cover of *Acropora* rubble and distance from the eastern tip of the island explained almost 90% of the variation in its abundance. *Acropora* alone explained 85% of the variation in *S. dorsopunicans* abundance ($r^2 = 0.842$, $p < 0.001$, Fig 5.8d). *S. diencaeus* showed no correlations between microhabitat characteristics and abundance at large spatial scales.

Table 5.5. Correlations between mean adult abundance and total live coral cover among the 13 sites. Data used in the correlation analysis were mean abundance at each site. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Species	r
<i>Stegastes planifrons</i>	0.87***
<i>Stegastes partitus</i>	0.25
<i>Stegastes diencaeus</i>	0.39
<i>Stegastes dorsoponicans</i>	0.09
<i>Microspathodon chrysurus</i>	0.54 ^{0.055}
<i>Sparisoma viride</i>	0.74**
<i>Sparisoma aurofrenatum</i>	0.43
<i>Scarus vetula</i>	0.62*
<i>Scarus rubripinne</i>	0.05
<i>Scarus iserti</i>	0.85***

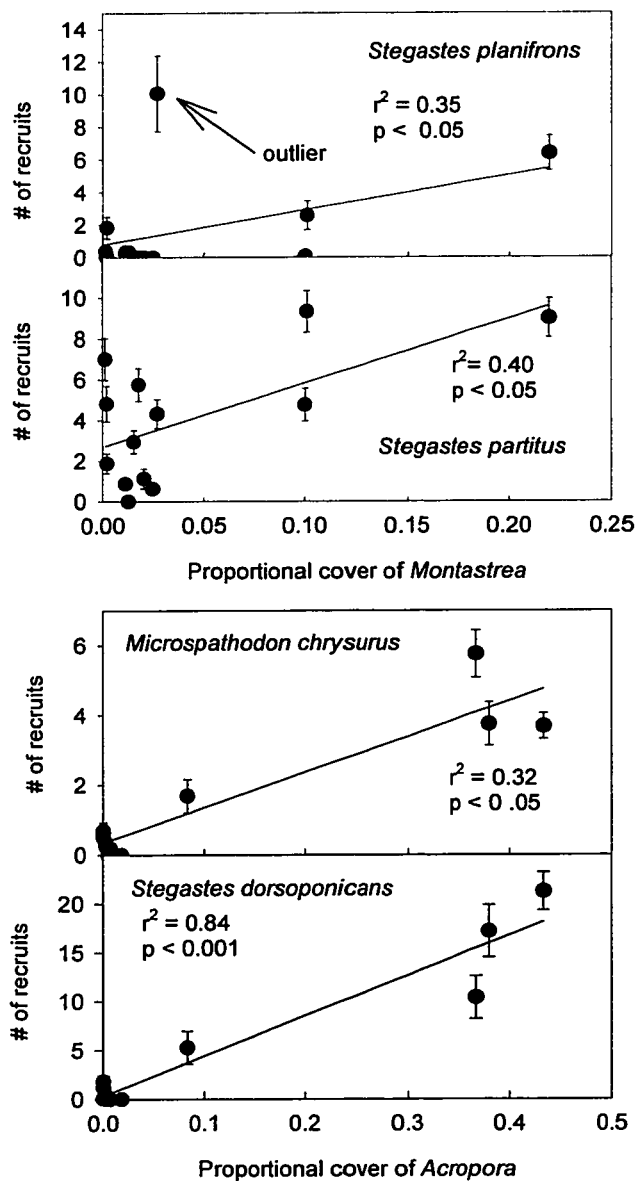


Figure 5.8. Relationship between microhabitat characteristics and abundance for 4 damselfish. These are final models with 'unexpected correlations' removed (see methods). Data are mean recruitment and mean percent cover of *Porites* at each site. Error bars indicate +1SE.

characteristics and abundance among patches (Table 5.4). *S. viride* abundance was correlated with the percent cover of *Porites* and *Acropora* rubble, but the correlation with *Porites* was positive when it was expected to be negative. If *Porites* is removed from the analysis, there is a non-significant relationship between distance from the eastern end of the island and *S. viride* abundance ($r^2 = 0.254$, $p = 0.08$). Likewise, the abundance of *S. iserti* was correlated with *Porites*, *Porites* rubble, and distance from the eastern tip of the island, but the correlations with *Porites* and *Porites* rubble were in the opposite direction from that expected by the analysis of small spatial scale microhabitat use. For example, within sites *S. iserti* associated with *Porites* rubble, but among sites their abundance was negatively correlated with the percent cover of *Porites* rubble. If these two substrata are removed from the analysis, abundance of *S. iserti* is negatively correlated with both *Acropora* rubble and distance from the eastern tip of the island. This relationship explains 51% of the variation in abundance ($r^2 = 0.512$, $p = 0.028$).

Four species showed positive correlations between abundance and total live coral cover (*Porites* + *Montastrea* + live coral) (Table 5.5). These species were *S. viride*, *S. vetula*, *S. iserti* and *S. planifrons*. The abundances of *S. dorsopunicans* and *M. chrysurus* were correlated among sites (Table 5.6), but no other damselfishes showed correlated distributions. The abundances of *S. viride*, *S. vetula*, and *S. iserti* were also correlated among sites (Table 5.6).

Table 5.6. Correlations between species abundance among sites for (a) damselfishes and (b) parrotfishes. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. Probabilities were Bonferroni adjusted within the SYSTAT statistical package.

Species	<i>S. planifrons</i>	<i>S. partitus</i>	<i>S. diencaeus</i>	<i>S. dorsop.</i>
<i>S. partitus</i>	0.416			
<i>S. diencaeus</i>	0.632	0.627		
<i>S. dorsopuncians</i>	0.228	-0.141	0.579	
<i>M. chrysurus</i>	0.622	0.016	0.626	0.840**

Species	<i>S. viride</i>	<i>S. aurofrenatum</i>	<i>S. rubripinne</i>	<i>S. vetula</i>
<i>S. aurofrenatum</i>	0.055			
<i>S. rubripinne</i>	0.468	0.028		
<i>S. vetula</i>	0.893***	0.010	0.615	
<i>S. iserti</i>	0.787**	0.105	0.262	0.755*

Discussion

Within patch microhabitat use

Non-random microhabitat use by benthic marine fishes is common in both coral reef (Sale et al. 1984a; Ebersole 1985; Eckert 1985; Tolimieri 1995; Caselle and Warner 1996) and temperate rocky reef systems (Holbrook et al. 1990; Carr 1991; Levin 1991, 1993, 1994b; Levin and Hay 1996). Consequently, it is not surprising that the majority of

scales. On the fore reef, eight of the 10 species demonstrated non-random microhabitat associations, while of the back reef all nine species that I examined associated with particular substrata. On the fore reef, two species, *S. diencaeus* and *S. dorsopunicans*, were randomly distributed. Why these two species neither associated with nor avoided particular substrata is impossible to determine from the present data. In the Caribbean, *S. dorsopunicans* (15 cm) is one of the larger damselfish, second in size only to *M. chrysurus* (20 cm). Adult *S. dorsopunicans* may be more or less free from predation pressure and not dependent on the substrata for predator avoidance to the degree that they show non-random microhabitat use. However, this hypothesis is difficult to reconcile with microhabitat association by the larger *M. chrysurus* and *S. dorsopunicans*' association with *Acropora* rubble on the back reef. The fore reef data show a similar pattern, although this pattern is not significant.

Non-random microhabitat use by newly recruited fish is often the result of selection during settlement (Sale et al. 1984a; Booth 1992; Tolimieri 1995) and presumably is important in providing shelter from predation (de Boer 1978; Roberts and Ormond 1987; Hixon and Beets 1989, 1993; Carr 1991) or from aggression by larger fishes (Sale 1972). On temperate reefs, access to food resources may be important as well (Levin 1994). For newly recruited fish, microhabitat may affect growth (Jones 1988a) and mortality (Jones 1988a; Tolimieri 1995), and as such, post-settlement processes can reinforce settlement patterns (Wellington 1992; Tolimieri 1995). For example, Jones (1988a) found that the coral substratum had a much larger effect on

interspecific competition. For adult fishes, correlative evidence suggests that the substratum can play an important role in providing shelter from predation (de Boer 1978; Roberts and Ormond 1987), nesting sites and food resources (Kaufman 1977). Experiments by Hixon and Beets (1989, 1993) on artificial reefs provide strong evidence that shelter size affects community structure and implicate predators as being important. These conclusions are supported by more recent work by Carr and Hixon (1995). Experiments by Robertson and Sheldon (1979) on patch reefs, however, suggest that shelter sites may not be limiting to population size.

My data show some qualitative relationships between potential shelter size and fish size for both damselfish and parrotfish. *Acropora* and *Porites* are both branching scleractinian corals, but *Acropora* produces much larger branches than *Porites* does, and piles of *Acropora* rubble have larger crevices and potential shelter holes than does *Porites* (pers. obs.). On the fore reef, *S. planifrons* (15 cm TL), and *M. chrysurus* (20 cm TL) associated with *Acropora* rubble more than *Porites* rubble, while the opposite was true for *S. partitus* (10 cm TL) (Robins et al. 1986). Likewise, the parrotfish appeared to use the substratum based on their relative size. On the fore reef all parrotfish associated with *Porites* rubble and avoided live *Porites*. This particular pattern is easily explained by the distribution of parrotfish food resources. Parrotfish feed on benthic algae which grows on *Porites* rubble among other substrata (Bruggemann 1994). However, the largest species (*S. vetula*, 61 cm TL) also associated with *Acropora* rubble, while the smaller species (*S. iserti*, 28 cm TL and *S. aurofrenatum*, 28 cm TL) appeared to avoid *Acropora* in favor of

rubripinne, 46 cm TL) (Robins et al 1986). For parrotfish, microhabitat use may be related to the different feeding patterns of different morphological groups with larger fishes feeding on different surfaces from smaller fishes (Bellwood and Choat 1990, Bruggemann et al. 1994a,b). Although predator avoidance may be important as well, it is probably more important at night than during the day. Parrotfish are known to make daily migrations from sleeping sites to feeding sites on some reefs when good feeding areas (shallow areas with high algal productivity) provide poor shelter (Buckman and Ogden 1973, Ogden and Buckman 1973).

If the scale and pattern of microhabitat use are the same for the adults and recruits of a species, adult distribution will likely reflect previous settlement and recruitment history. However, the scale at which species interact with the substratum often increases as fish grow larger (Tolimieri in press, pers. obs.), and some species undergo ontogenetic shifts in habitat or microhabitat use (Eggleston 1995; Green 1996), so the picture is probably more complicated at the within reef scale. For example, although *S. planifrons* preferentially settle to *Montastrea annularis* on the back reef of Tague Bay (Tolimieri 1995), adult fishes in the same habitat associated with *Acropora* rubble, not *Montastrea*. Therefore, *S. planifrons* distributions on the back reef resulted from (1) fish moving from *Montastrea* to *Acropora* at some point in the life-cycle, or (2) from differential survival on the two substrata at some point after recruitment to the benthic habitat. Likewise Nassau grouper, *Epinephelus striatus*, recruits initially to *Porites* spp. covered by masses of macroalgae but eventually moves to other substrata (Eggleston 1995). In cases where

within reef pattern of adult distribution will likely reflect adult requirements and not recruitment history.

Overall, microhabitat use was consistent between the two habitats (fore reef and back reef at Tague Bay). There were some differences, but these differences are easily explained and unimportant to the overall picture. For example, on the fore reef, *S. planifrons* associated with *Acropora* rubble in both habitats, but its association with *Porites* rubble varied between habitats. However, as Figure 4 shows, by using more *Porites* rubble, *S. planifrons* was avoiding areas comprised of pavement or sand. It was positively associated with *Montastrea* in both habitats (on the back reef *Montastrea* loaded on the third canonical variate). All parrotfish species associated with *Porites* rubble on the fore reef and appeared to avoid live *Porites*. As discussed above, this pattern of microhabitat use can be attributed to parrotfish grazing on the algae growing on the dead *Porites* rubble. In both habitats, however, the species separated on an axis defined by *Acropora* rubble and *Porites* rubble in the same general way. The only exception was that *S. viride* associated with *Acropora* rubble on the back reef while showing no relationship on the fore reef. Live *Porites* was less abundant on the back reef than on the fore reef (10% cover vs. 27% cover), and avoidance of live *Porites* was not a factor.

Several studies have found correlations between habitat or microhabitat characteristics and adult density, but these studies have generally focused on only one spatial scale. Characteristics such as reef height (Thresher 1983), depth (Thresher 1983), reef size (Warner and Hoffman 1980), topographic complexity (Luckhurst and Luckhurst 1978; Thresher 1983; Roberts and Ormond 1987), and live coral cover (Bell and Galzin 1984; Bell et al. 1985) have been shown to be correlated with adult density. Roberts and Ormond (1987) did address spatial scale and noted that topographic complexity predicted fish abundance along 200 m transects but not along smaller 10 x 2 m transects.

Several studies have specifically addressed the interaction between microhabitat use and abundance across spatial scales, but their results are mixed. Caselle and Warner (1996) found that the microhabitat characteristics explained abundance of *Thalassoma bifasciatum* along transects (20 x 2 m), but these same microhabitat characteristics did not explain recruitment among sites located along the north coast of St. Croix, USVI. In fact, some correlations were the reverse of what they expected based on their small spatial scale data. Likewise, Tolimieri (1995) saw no relationship between microhabitat choice during settlement for *S. planifrons* and recruitment to ten sites around three islands, but variation among sites in *Montastrea annularis*, *S. planifrons*' preferred substratum, was low. However, Tolimieri (in press) found that for *S. viride* recruitment to the same sites was correlated with microhabitat use by recruits in 3 out of 4 years.

In the present study, the most important question was whether within patch microhabitat use predicted the distribution and abundance of fishes among patches. Any

potential to be obscured or overridden by processes that function at the larger spatial scale (Tolimieri 1995; Caselle and Warner 1996). My data show mixed results, which appear to have some taxonomic basis. For the damselfishes, four of the five species that I tested showed correlations between small scale microhabitat use and large scale abundance. These large scale relationships explained between 32 - 49% of the variation in the abundance of these three species and up to 85% of the variation in a fourth. However, all five parrotfish species used the substratum non-randomly within sites. However, only *S. iserti* showed a relationship between microhabitat characteristics and abundance among sites. It is difficult to distinguish between microhabitat use and oceanic processes that influence larval supply because its abundance was also correlated with distance from the eastern tip of the island.

Why was there no relationship between microhabitat use and large spatial scale abundance for some species? There are at least three possibilities: 1) small scale patterns of microhabitat use may be obscured by large scale processes that influence the rate of replenishment of these populations; 2) ontogenetic changes in microhabitat use may also obscure any relationship between adult microhabitat use and abundance; and 3) small scale microhabitat use varies among sites.

There is evidence that suggests that adult population size is directly correlated to past recruitment (Doherty and Fowler 1994a,b) and that recruitment is correlated with larval supply (Victor 1984, 1986; Milicich et al. 1994; Williams et al. 1994). Processes that influence larval supply generally function at spatial scales greater than one patch.

stochastic weather events (Shenker et al. 1993; Sponaugle and Cowen 1996), and tidal cycles. There is some evidence to suggest that larvae can control their vertical and horizontal distribution in the water column (Kobayashi 1989; Leis 1994; Sponaugle and Cowen 1996; Stobutzki and Bellwood 1994) and, therefore, control their dispersal to some extent, but the degree to which larval fish control their own destination is unknown.

Correlations between adult microhabitat use and large scale patterns of abundance may be further obscured if there are ontogenetic changes in habitat and microhabitat requirements (Eggleston 1995; Green 1996). In these cases, variation in adult abundance at larger spatial scales may be based on the microhabitat requirement of the recruits. For example, Tolimieri (in press) found that *S. viride* recruits associated with the coral *Porites porites*. The abundance of live and dead *Porites* at 10 sites around 3 islands predicted the abundance of recruits in 3 out of 4 years. Contemporary adult populations were correlated with the pattern of recruitment, which was stable through time. In the present study, the distribution of adult *S. viride* was not correlated with adult microhabitat use, but adult *S. viride* were correlated with the abundance of the recruit's substratum *Porites*. In this situation, large scale patterns of adult abundance may be the result of microhabitat choice during settlement or a bottleneck effect on the survival of newly recruited fish.

Finally, small scale microhabitat use for some species may vary among sites depending upon what substrata are available. By quantifying microhabitat use at only general location (Tague Bay), I may have missed more important or stronger patterns

may have been important at large scales. This is an important point and demonstrates the need to further replicate this type of approach at other locations. It also implies that making broad conclusions based on only one site or study is dangerous.

We might expect to find relationships between adult microhabitat use and large scale abundance under two conditions: (1) if microhabitat requirements are strong, or (2) if adult and juvenile microhabitat preferences are similar. For adults, space does not appear to be limiting on reefs, although subcomponents of the population may be affected (e.g. breeding sites may limit the number of individuals that breed, but not the overall population size) (Robertson and Sheldon 1978; Robertson et al. 1981; Jones 1991). However, some species do show strong microhabitat requirements (Forrester 1990; Doherty and Fowler 1994b; Booth 1995), and microhabitat can affect growth (Jones 1988a). In *S. planifrons*, adults and recruits use similar substrata. Although adults also used *Acropora*, both ages used *Montastrea* (Tolimieri 1995, present study), and 35% of the distribution of adult fishes among patches was explained by the percent cover of *Montastrea*. In contrast, *S. aurofrenatum* recruits were randomly distributed with respect to the substrata (Tolimieri, unpublished data), and *S. aurofrenatum* adults showed no correlation whatsoever with microhabitat characteristics. The abundance of four out of the ten species was correlated with total live coral cover, suggesting that habitat quality was important to these fishes in a more general way.

Robertson (1995, 1996) has recently demonstrated strong interspecific competition in the same set of Caribbean damselfish species. In general, he found that

that the reverse was not true. It is interesting, therefore, that the abundance of these three species was positively correlated among sites (though non-significant) suggesting that interspecific competition may not be important at this spatial scale. Likewise, parrotfish abundance was either positively correlated among sites or non-significant (but positive).

Thus, these data show that microhabitat use within patches can determine or predict significant amounts of the variation in fish abundance among patches at larger spatial scales for some but not all species. Whether or not microhabitat characteristics are important appears to have a taxonomic basis and probably results from how the individuals of various species interact with the substratum. These results also demonstrate that managers working in this system need to consider not only the microhabitat characteristics of individual sites, but how individual species of fish interact with those microhabitat characteristics across a number of spatial scales.

Patchiness and spatial scale are factors that pervade ecology and our understanding of the processes that determine distribution and abundance. These factors are related to a broad number of topics from predator-prey dynamics (e.g. Huffaker 1958; Caswell 1978), to niche theory (MacArthur 1957), island biogeography (MacArthur and Wilson 1967), and metapopulation theory (Levins 1969; Hanski et al. 1991), whether or not they are incorporated directly into specific theories, hypotheses or models. It is impossible to understand how populations, assemblages, and communities operate without considering patchiness and spatial scale because they often influence the importance of other factors. Within this context, it is essential to determine whether factors that are important at smaller spatial scales 'scale up' to influence population and community dynamics at larger scales. Alternatively, entirely different processes may explain community structure or the distribution and abundance of a species at larger spatial and temporal scales. In the present study, I examined the effects of these two factors on aspects of the population dynamics of Caribbean coral reef fishes. I have demonstrated that not all patches are equally likely to be replenished in a system where replenishment from external sources is essential to the persistence of the population. I found that microhabitat use within patches by individual fishes could predict both recruitment and adult abundance among patches at scales up to 70+ kilometers.

Most ecological systems are patchy across a myriad of spatial scales. These scales probably defy a specific definition and should be defined for each species (Southwood 1977). We can, however, recognize at least two, non-continuous spatial

substrata can be distributed within the home range of an individual, such that the individual may utilize more than one patch. Moving up in scale, isolated patches of suitable habitat that encompass the home ranges of a number of individuals can exist as a larger system of patches.

Regardless of the specific definition of a patch, environmental heterogeneity may promote coexistence of species by allowing different species to utilize different habitat niches in otherwise overlapping distributions (Gause 1937; Hutchinson 1957; MacArthur 1957; Ebersole 1985; Morris 1996). Disturbed patches promote coexistence by providing refugia for inferior competitors to colonize and reproduce in prior to being displaced by competition during succession (Sousa 1979a,b; Connell 1978; Whitman 1987).

Likewise, patchy environments allow the coexistence of predators and prey because prey can disperse to patches that are unoccupied by predators and reproduce in those patches before being eventually driven extinct locally by predation (Huffaker 1958; Caswell 1978). Assemblage or community structure may be determined by which species are present to colonize recently opened patches (Sale 1974, 1977; Hubbell 1979; Sousa 1979a,b). Recently, ecologists have begun to examine how local extinction within patches and movements between patches of suitable habitat influence the distribution of 'metapopulations' at large spatial scales and through time (Hanski and Gilpin 1991; Hanski et al. 1991). Metapopulation ideas have been applied to host-parasite interactions (Overton 1994), conservation (Lahaye et al. 1994) and even marine fisheries (Man et al. 1994). The persistence of a species through time among isolated patches of habitat is

the dynamics of the local populations within each habitat patch. This conclusion has obvious consequence for the conservation of species (McNiell and Fairweather 1993).

Scale is also an important factor in the study of ecology because different processes can be important at different spatial or temporal scales. This observation is especially important when combined with patchiness. Different processes may determine population size and community structure within patches and the distribution and abundance among patches. At the smaller ecological spatial scales, processes like habitat selection or use (Sale 1984a; Tolimieri 1995; Morris 1996) and competition (Connell 1960; Werner et al. 1977; Connell 1983; Jones 1987a,b, 1988; Forrester 1995; Robertson 1995, 1996) can affect the growth, mortality and distribution of individuals within a patch of habitat. However, these processes are limited to functioning within patches of habitat. For example, individuals within one patch cannot compete or interact with those in another patch. At larger scales, other factors may be more important in determining the distribution and abundance of a species or the composition of an assemblage or community (i.e., individuals located in different patches cannot compete with one another). For example, physiological stress, disturbance and light are important in delineating zones in marine systems (Connell 1960; Menge and Sutherland 1987; Witman 1987). Disturbance may open up patches of habitat such that the coexistence of species at larger scales may be made possible by the continual re-setting of succession (Sousa 1979a,b; Connell 1978). In patchy habitats, processes that influence dispersal among patches may be of critical importance. Marine communities are excellent examples of

patches appear to limit local population size for a number of organisms (Yoshioka 1982; Menge and Sutherland 1987; Roughgarden et al. 1988; Hughes 1990; Sutherland 1990; Minchinton and Scheibling 1991; Doherty and Williams 1994a,b). At even larger spatial scales, biogeographic patterns may be more related to historical events in geological time than to current species requirements, biology or interactions (Tivy 1992).

Dispersal is closely connected to both spatial scale and patchiness. Dispersal and successful establishment are important factors in a number of ecological realms of thought, in particular, island biogeography (MacArthur and Wilson 1967) and metapopulation dynamics (Levins 1968; Hanski et al. 1991). In marine systems, recruitment is an important force influencing population size and community structure both within and among patches (Yoshioka 1982; Menge and Sutherland 1987; Roughgarden et al. 1988; Hughes 1990; Sutherland 1990; Doherty 1991; Minchinton and Scheibling 1991; Doherty and Williams 1994a,b).

I examined factors that influence the distribution and abundance of coral reef fishes within and among patches and across a number of spatial scales. In particular, I questioned whether or not some patches were more likely to be replenished than others (receive recruitment or in a metapopulation context, achieve successful immigration), and whether microhabitat use by individual fishes influenced the large scale distribution of these fishes (Chapter 2, 3 & 5). My data show that processes that function at smaller spatial scales (i.e. within patches of habitat) correlate the distribution and abundance of

should not be generalized to all species.

Some species had recruitment patterns that were spatially consistent through time (Chapter 2). Microhabitat use at the level of the individual recruit explained much of this variation in recruitment for the stoplight parrotfish (Chapter 3). Microhabitat use by adult fishes of a number of species explained some of the variation in adult abundance, in particular for damselfish. Again, these results demonstrate that patch quality (abundance of various substrata) can predict the distribution and abundance of a species among patches (Chapter 5). However, this conclusion should not be generalized to all species. For example, in Chapter 2, I found that 8 of 14 species had recruitment patterns whose spatial pattern varied through time. Microhabitat use could not explain variation in the abundance of adult parrotfish (Chapter 5).

Why small scale microhabitat use did or did not explain abundance at larger spatial scales is probably related to 1) how the fish interacts with the substratum, and 2) the ontogeny of microhabitat use. For example, evidence from Chapter 4 suggests that patterns of microhabitat use for *Sparisoma viride* were established by post-settlement processes that affected either mortality, movement of new recruits, or both. If patch quality influences mortality we might expect to see good correlations between microhabitat use and abundance. However, if microhabitat simply distributes fish within a habitat patch onto different substrata, but substratum is not limiting, then we should not expect to see relationships at large scales. Instead, processes that influence the delivery

scale of microhabitat use or substratum preferences may also disrupt relationships.

My work demonstrates the need to examine the ecology of a number of species across a number of spatial scales prior to drawing general conclusions about how different factors influence either population or community dynamics. Processes like microhabitat use that function within isolated patches of habitat can influence the population dynamics of a species at larger spatial scales for some species. Whether or not this conclusion is true depends on the individual species and how it interacts with the benthic environment. This is an especially important conclusion for resource managers who will need to understand the ecology of target species prior to establishing reserves for the conservation of particular species and biodiversity in general.

- Aldenhoven, J.M., 1986. Local variation in mortality rates and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Mar. Biol. 92: 237-244.
- Andrewartha, H.G. & L.C. Birch, 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Bailey, K.M. 1981. Larval transport and recruitment of Pacific hake *Merluccius productus*. Mar. Ecol. Prog. 6:1-9.
- Bell, J. D., Harmelin--Vivien, M. L., & Galzin, R. 1985. Large scale spatial variation in abundance of butterflyfishes (Chaetodontidae) on Polynesian reefs. Proc. Int. Coral Reef Congr. 5: 421-426.
- Bell, J. D., & Galzin, R. 1984. Influence of live coral cover on coral-reef fish communities. Mar. Ecol. Prog. Ser. 15: 265-274.
- Bellwood, D. R., & Choat, J. H. 1990. A functional analysis of grazing in parrotfishes (family Scaridae). Envir. Biol. Fishes 28: 189-214.
- Booth, D.J. 1992. Larval settlement patterns and preferences by domino damselfish *Dascyllus albisella* Gill. J. Exp. Mar. Biol. Ecol. 155: 85-104.
- Booth, D. J. 1995. Juvenile groups in a coral reef damselfish: density-dependent effects on individual fitness and population demography. Ecology 76:91-106

- of pomacentrid reef fish in the US Virgin Islands. *Coral Reefs* 13:81-89.
- Brokaw, N.V. 1985a. Treefalls, regrowth, and community structure in tropical forests. .. 53-79. *In*: S.T.A. Pickett & P.S. White. *Natural disturbance: and evolutionary perspective*. Academic Press, New York.
- Brokaw, N.V. 1985b. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682-687.
- Brothers, E.B., D.McB. Williams, & Sale, P.F. 1983. Length of larval life cycle in twelve families of fishes at "One Tree Lagoon", Great Barrier Reef, Australia. *Mar. Biol.* 76: 319-324.
- Bruggemann, J.H., Begeman J., Bosma, E.M., Verberg, P. & A.M. Breeman. 1994a. Foraging by the stoplight parrotfish *Sparisoma viride*. II. Intake and assimilation of food, protein, and energy. *Mar. Ecol. Prog. Ser.* 106:57-71.
- Bruggemann, J.H., Kuyper, M.W.M. & A.M Breeman 1994b. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Mar. Ecol. Prog. Ser.* 112: 51-66.
- Bruggmann, J.H., van Oppen, M.J.H. & A.M. Breeman, 1994c. Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Mar. Ecol. Prog. Ser.* 106: 41 - 55.
- Buckman, N.S. & J.C. Ogden, 1973. Territorial behavior of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54: 1377-1382.

- intertidal barnacles. *Ecol. Monogr.* 55:313-332.
- Caley, M.J. 1995. Reef-fish community structure and dynamics: an interaction between local and larger-scale processes? *Mar. Ecol. Prog. Ser.* 129: 19-29.
- Carr, M. H. 1991. Habitat selection and recruitment of an assemblage of temperate zone reef fishes. *J. Exp. Mar. Biol. Ecol.* 146:113-137.
- Carr, M.H. 1994a. Effects of macroalgal dynamics on recruitment of a temperate reef fish. *Ecology* 75:1320-1333.
- Carr, M.H. 1994b. Predicting the response of recruitment of temperate reef fishes to changes in macrophyte density caused by disturbance. pp. 255-270 *In*: Stouder, D.J., Fresh, K., & R.J. Feller. *Theory and Application in the Feeding Ecology of Fishes*, Belle Baruch Marine Institute Series, University of South Carolina Press, Columbia.
- Carr, M. H., & M. A. Hixon 1995. Predation effects on early post-settlement survivorship of coral-reef fishes. *Mar. Ecol. Prog. Ser.* 124: 31-42.
- Caselle, J.E. & R.R. Warner 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77: 2488-2504.
- Caswell, H. 1978. Predator-mediated coexistence: a non-equilibrial model. *Am. Nat.* 112: 127-154.
- Clarke, R.D. 1992. Effects of microhabitat and metabolic rate on food intake, growth and fecundity of two competing coral reef fishes. *Coral Reefs* 11: 199-205.

reef. Mar. Ecol. Prog. Ser. 137: 51-58.

- Clifton, K.E. 1989. Territory sharing by the Caribbean striped parrotfish, *Scarus iserti*: patterns of resource abundance, group size and behavior. Anim. Beh. 37: 90-103.
- Clifton, K.E. 1990. The costs and benefits of territory sharing of the Caribbean coral reef fish, *Scarus iserti*. Behav. Ecol. Sociobiol. 26: 139-147.
- Clifton, K.E. 1991. Subordinate group members act as food-finders within striped parrotfish territories. J. Exp. Mar. Biol. Ecol. 145: 141-148.
- Clifton, K.E. 1995. Asynchronous food availability on neighboring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. Mar. Ecol. Prog. Ser. 116: 39-46.
- Coe, W.R. 1953. Resurgent populations of littoral marine invertebrates and their dependence on ocean currents and tidal currents. Ecology 34: 225-229.
- Coe, W.R. 1956. Fluctuations in populations of littoral marine invertebrates. J. Mar. Res. 15: 212-232.
- Connell, J.H. 1978. Diversity in tropical rainforests and coral reefs. Science 199: 1302-1310.
- Connell, J.H. 1983. On the prevalence and importance of interspecific competition: evidence from field experiments. Am. Nat. 122: 661-696.

- settlement mortality in rocky intertidal communities. J. Exp. Mar. Biol. Ecol. 71:11-45.
- Cowen, R.K. 1985. Large scale pattern of recruitment by the labrid, *Semicossyphus pulcher*: causes and implications. J. Mar. Res. 43: 719-742.
- Cowen, R.K. & L.R. Castro 1994. Relation of coral reef fish larval distributions to island scale circulation around Barbados, West Indies. Bull. Mar. Sci. 54: 228-244.
- Danilowicz, B.S. 1996. Choice of coral species by naive and field-caught damselfish. Copeia. 735: 00-00.
- Danilowicz, B.S. in press. A potential mechanism for the episodic recruitment of a coral reef fish. Ecology (in press).
- Dayton, P.K. 1985. The ecology of kelp communities. Annu. Rev. Ecol. Syst. 16: 215-245.
- de Boer, B.A. 1978. Factors influencing the distribution of the damselfish *Chromis cyanea* (Poey), Pomacentridae, on a reef at Curacao, Netherlands Antilles. Bull. Mar. Sci. 28: 550-565.
- Doherty, P.J. 1980. Biological and physical constraints on the populations of two sympatric territorial damselfishes on the southern Great Barrier Reef. Unpublished Ph.D. dissertation, University of Sydney, Sydney, Australia.
- Doherty, P.J. 1981. Coral reef fishes: recruitment limited assemblages? Proc 4th Int Coral Reef Symp 2: 465-470.

- territorial damselfish. J. Exp. Mar. Biol. Ecol. 65: 249-261.
- Doherty, P.J. 1983. Tropical territorial damselfishes: is density limited by aggression or recruitment. Ecology 64: 176-190.
- Doherty, P.J., 1987. The replenishment of populations of coral reef fishes, recruitment surveys, and the problems of variability manifest on multiple scales. Bull. Mar. Sci. 41: 411-422.
- Doherty, P.J. 1988. Large-scale variability in the recruitment of a coral reef fish. Proc. Int. Coral Reef Symp., 6th. 2:667-672.
- Doherty, P.J. 1991. Spatial and temporal patterns in recruitment. pp. 261-293. In: P. F. Sale. The ecology of coral reef fishes. Academic Press, New York, NY.
- Doherty, P.J. & A. Fowler. 1994a. An empirical test of recruitment limitation in a coral reef fish. Science. 263: 935-39.
- Doherty, P.J. & A. Fowler. 1994b. Demographic consequences of variable recruitment to coral reef fish populations: a congeneric comparison of two damselfishes. Bull. Mar. Sci. 54: 297-313.
- Doherty, P.J., Kingsford, M., Booth, D. & J. Carleton 1996. Habitat selection before settlement by *Pomacentrus coelestis*. Mar. Freshwater Res. 47: 391-9.
- Doherty, P.J. & D.McB. Williams 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26:487-551.

- the reef fish *Eupomacentrus leucostictus*. Am. Nat. 115: 492-509.
- Ebersole, J.P. 1985. Niche separation of two damselfish species by aggression and differential microhabitat utilization. Ecology 66: 14-20.
- Eckert, G.J. 1984. Annual and spatial variation in recruitment of labroid fishes among seven reefs in the Capricorn/Bunker Group, Great Barrier Reef. Mar. Biol. 78: 123-127.
- Eckert, G.J. 1985. Settlement of coral reef fishes to different natural substrata and at different depths. 5th Int. Coral Reef Conf., Tahiti 5: 385-390.
- Eckert, G.J. 1987. Estimates of adult and juvenile mortality for labrid fishes at One Tree Reef, Great Barrier Reef. Mar. Biol. 95: 167-171.
- Eggleston, D.B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar. Ecol. Prog. Ser. 124: 9-22.
- Ehrlich, P.R. 1975. The population ecology of coral reef fishes. Annu. Rev. Ecol. Syst. 6: 211-247.
- Forrester, G.E. 1988. Post-recruitment demographic processes in a coral reef fish: Their importance in the regulation and determination of population size. Masters Thesis, Univ. of Sydney.
- Forrester, G.E. 1990. Factors influencing the juvenile demography of a coral reef fish. Ecology 71: 666-681.

- of food consumption by humbug damselfish, *Dascyllus aruanus*. Anim. Behav. 42: 701-711.
- Forrester, G.E. 1995. Strong density-dependent survival and recruitment regulate the abundance of a coral reef fish. Oecologia 103: 275-282.
- Fowler, A.J., Doherty, P.J. & D.McB. Williams 1992. Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 82:131-141.
- Gaines, S., Brown & J. Roughgarden 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. Oecologia 67: 267-272
- Gaines, S., & J. Roughgarden 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. Proc. Natl. Acad. Sci. 82: 3707-3711.
- Garcia-Rubies, A. & E. Macpherson 1995. Substrate use and temporal pattern of recruitment in juvenile fishes of the Mediterranean littoral. Mar. Biol. 124: 35-42.
- Gause, G.F. 1937. Experimental populations of microscopic organisms. Ecology: 18: 173-79.
- Gladstone, W. & M. Westoby 1988. Growth and reproduction in *Canthigaster valentini* (Pisces, Tetradontidae): A comparison of a toxic reef fish with other reef fishes. Envir. Biol. Fishes 21: 201-221.

- 154 *In* O.A. Jones & R. Endean. Biology and Geology of Coral Reefs. Vol. 3. Academic Press, New York.
- Green, A.L. 1996. Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Mar. Ecol. Prog. Ser.* 133: 1-11.
- Hadfield, M.G. 1986. Settlement and recruitment of marine invertebrates: A perspective and some proposals. *Bull. Mar. Sci.* 39: 418-28.
- Hanski, I., & Gilpin, M. 1991. Metapopulation dynamics: brief history and conceptual domain. *Biol. J. Linnean Soc.* 42: 3-16.
- Hanski I., Kouki, J. & A. Halkka, 1995. Three explanations of the positive relationship between distribution and abundance of species. pp. 108-116 *In*, Species diversity in ecological communities. edited by R. E. Ricklefs & D. Schluter. Chicago Press, Chicago.
- Haury, L. R., McGowan, J. A., and Weibe, P. H. 1978. Patterns and processes in the time-space scales of plankton distributions. pp. 277-327 *In*: J. H. Steele. Spatial pattern in plankton communities. Plenum, New York.
- Hixon, M.A. 1991. Predation as a process structuring coral reef fish communities. pp. 475-508 *In*: P.F. Sale. The ecology of fishes on coral reefs. Academic Press, San Diego.
- Hixon, M.A. & J.P. Beets 1989. Shelter characteristics and Caribbean fish assemblages: experiments with artificial reefs. *Bull. Mar. Sci.* 44: 666-680.

fish communities. Ecol. Monogr. 63: 77-101.

Hjort, J. 1914. Fluctuations in the great fisheries of Northern Europe. Rep. Proc. Con. Int. Exp. Mer. 20: 1-13.

Hobson, E.S. 1991. Trophic relationships of fishes specialized to feed on zooplankters above coral reefs. pp. 69- -95 *In*, P.F. Sale. The ecology of fishes on coral reefs. Academic Press, Inc., San Diego, California.

Hobson, E.S. & J.R. Chess 1978. Trophic relationships among fishes and plankton in the lagoon at Enewtak Atoll, Marshall Islands. Pac. Sci. 40: 7-26.

Holbrook, S.J., Carr, M.H., Schmitt, R.J. & J.A. Coyer 1990a. Effect of giant kelp on local abundance of reef fishes: the importance of ontogenetic resource requirements. Bull. Mar. Sci. 47: 104-114.

Holbrook, S.J., Schmidt, R.J. & R.F. Ambrose. 1990b. Biogenic habitat structure and characteristics of temperate reef fish assemblages. Aust. J. Ecol. 15: 489-503.

Hubble, S.P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science. 203: 1299-1309.

Huffaker, C.B. 1958. Experimental studies on predation: dispersion factors and predator-prey oscillations. Hilgardia 27: 343-383.

Hughes, T.P. 1990. Recruitment limitation, mortality, and population regulation in open systems: a case study. 71: 12-20.

- Demography. Cold Spring Harbor Symposia on Quantitative Biology 22: 415-27.
- Itzkowitz, M. 1990. Heterospecific intruders, territorial defense and reproductive success in the beaugregory damselfish. J.Exp. Mar. Biol. Ecol. 140: 49-56.
- Jones, G.P. 1986. Food availability affects growth in a coral reef fish. Oecologia 70: 136-139.
- Jones, G.P. 1987a. Competitive interactions among adults and juveniles in a coral reef fish. Ecology 68: 1534-1547.
- Jones, G.P. 1987b. Some interactions between residents and recruits in two coral reef fishes. J. Exp. Mar. Biol. Ecol. 114: 169-182.
- Jones, G. P. 1988a. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. J. Exp. Mar. Biol. Ecol. 123: 115-126.
- Jones, G.P. 1988b. The ecology of rocky reef fish of north-eastern New Zealand: a review. New Zealand J. Mar. Freshw. Res. 22: 445-462.
- Jones, G.P. 1990. The importance of recruitment to the dynamics of a coral reef fish population. Ecology 71: 1691-1698.
- Jones, G.P. 1991. Postrecruitment processes in the ecology of coral reef fish populations. pp. 294 - 328 *In*: P.F. Sale. The ecology of fishes on coral reefs. San Diego, Academic Press.

- coral reefs. Proc. Int. Coral Reef Symp. 3rd: 559-564.
- Keough, M.J. & B.J. Downes 1982. Recruitment of marine invertebrates: the role of active larval choice and early mortality. *Oecologia* 54: 348-352.
- Kingsford, M. J., & J.H. Choat 1986. Influence of surface slicks on the distribution and onshore movements of small fish. *Mar. Biol.* 91: 161-171.
- Kobayashi, D.R. 1989. Fine-scale distribution of larval fishes: Patterns and processes adjacent to coral reefs in Kaneohe Bay, Hawaii. *Mar. Biol.* 100: 285-293.
- Koltes, K.H. 1993. Aspects of the reproductive biology and social structure of the stoplight parrotfish, *Sparisoma viride*, at Grand Turk, Turks and Caicos Islands, B.W.I.. *Bull. Mar. Sci.* 52: 729-805.
- Krebs, C.R. 1978. *Ecology: The experimental analysis of distribution and abundance.* Harper and Row, New York.
- LaHaye, W.S., Gutierrez, R.J. and H. R. Akcakaya 1994. Spotted owl metapopulation dynamics in Southern California. *J. Anim. Ecol.* 63: 775-785.
- Leis, J.M. 1994. Coral Sea atoll lagoons: closed nurseries for the larvae of a few coral reef fishes. *Bull. Mar. Sci.* 54: 206-227.
- Leis, J. M. 1991. The pelagic stage of reef fishes: the larval biology of coral reef fishes. pp. 183 - 230 *In*: P.F. Sale. *The ecology of fishes on coral reefs.* San Diego, Academic Press.

- Lizard Island, Great Barrier Reef. *Mar. Biol.* 90: 505-516.
- Levin, P.S. 1991. Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. *Mar. Ecol. Prog. Ser.* 75: 183-189.
- Levin, P.S. 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. *Oecologia* 94: 176-185.
- Levin, P.S. 1994a. Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. *Env. Biol. Fish.* 40:271-281.
- Levin, P.S. 1994b. Fine-scale recruitment variation in a temperate demersal fish: the importance of settlement versus post-settlement processes. *Oecologia* 97: 124-133.
- Levin, P.S. 1996. Recruitment in a temperate demersal fish: Does larval supply matter? *Limnol. Oceanogr.* 41: 672-679.
- Levin, P.S. & M.E. Hay 1996. Responses of temperate reef fishes to alterations in algal structure and species composition. *Mar. Ecol. Prog. Ser.* 1334: 37-47.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15: 237-240.
- Luckhurst, E., & Luckhurst, K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* 49:317-323.
- MacArthur, R.H. 1957. On the relative abundance of bird species. *Proc. Nat. Acad. Sci. U.S.A.* 43: 293-95.
- MacArthur, R.H. & E.O. Wilson 1967. The theory of island biogeography. Princeton University Press, Princeton N.J.

- Mar. Ecol. Prog. Ser. 114: 211-218.
- Man, A., Law, R. & N.V.C. Polunin 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biol. Conserv. 71: 197-204.
- McFarland, W.N., Brothers, E.B. Ogden, J.C. Shulman, M.J. Bermingham, E.L. & N.M. Kotchian-Prentiss 1985. Recruitment patterns of young French grunts, *Haemulon flavolineatum* (family Haemulidae) at St. Croix, U.S.V.I. Fish. Bull. 83: 413-426.
- McGehee, M.A. 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth, and substrate size off Puerto Rico. Mar. Ecol. Prog. Ser. 105: 243-255.
- McGehee, M.A. 1995. Juvenile settlement, survivorship and in situ growth rates of four species of Caribbean damselfishes in the genus *Stegastes*. Env. Biol. Fishes. 44: 393-401.
- McNiell, S.E. and P.G. Fairweather 1993. Single large or several small marine reserves? An experimental approach with seagrass fauna. J. Biogeogr. 20: 429-440.
- Meekan, M.G., Milicich, M. J., & P.J. Doherty 1993. Larval production drives temporal patterns of larval supply and recruitment of a coral reef damselfish. Mar. Ecol. Prog. Ser. 93: 217-225.
- Meekan, M.G. Steven, A.D. & M.J. Fortin 1995. Spatial patterns in the distribution of damselfishes on a fringing coral reef. Coral Reefs 14: 151-161.

competition, and predation in relation to environmental stress and recruitment.

Am. Nat. 130: 730-757.

Milicich, M.J., Meekan, M.G., & P.J. Doherty 1992. Larval supply, a good predictor of recruitment of three species of reef fish (Pomacentridae). Mar. Ecol. Prog. Ser. 86: 153-166.

Milicich, M.J. & P.J. Doherty 1994. Larval supply of coral reef fish populations: Magnitude and synchrony of replenishment to Lizard Island, Great Barrier Reef. Mar. Ecol. Prog. Ser. 110: 121-134.

Minchinton, T.E. & R.E. Scheibling 1991. The influence of larval supply and settlement of the population structure of barnacles. Ecology 72: 1867-1879.

Morgan, S.G., Zimmer-Faust, R.K, Heck, K.L. Jr. & L.D. Coen. 1996. Population regulation of blue crabs *Callinectes sapidus* in the northern Gulf of Mexico: postlarval supply. Mar. Ecol. Prog. Ser. 133: 73-88.

Morris, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. Ecology 77: 2352-2364.

Moyer, J.T., Thresher, R.E., and C.L. Colin 1983. Courtship, spawning, and inferred social organization of American angelfishes (Genera *Pomacanthus*, *Holocanthus*, and *Centropyge*; *Pomacanthidae*). Env. Biol. Fish. 9: 25-29.

Nagelkerken, W. 1977. The distribution of the grasby *Petrometopon cruentatum* (Lacepede) on the coral reef at the southwest coast of Curacao. Proc. Int. Coral Reef Symp. 3rd, Miami, Florida: 311-315.

- of the striped parrotfish, *Scarus croicensis* Bloch (Scaridae). Ecology 54: 589-596.
- Overton, J.McC. 1994. Dispersal and infection in mistletoe metapopulations. J. Ecol. 82: 711-723.
- Peterson, C.H. & H.C. Summerson 1992. Basin-scale coherence of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. Mar. Ecol. Prog. Ser. 90: 257-272.
- Peterson, C.H., Summerson, H.C. & R.A. Leutich Jr. 1996. Response of bay scallops to spawner transplants: a test of recruitment limitation. Mar. Ecol. Prog. Ser. 132: 93-107.
- Pfister, C.A. 1996. The role and importance of recruitment variability to a guild of tide pool fishes. Ecology. 77: 1928-1941.
- Pitcher, C.R. 1988. Spatial variation in the temporal pattern of recruitment of a coral reef damselfish. Proc. Int. Coral Reef Symp., 6th. 2: 811-816.
- Planes, S. Levefre, A., Legendre, P. & R. Galzin, 1993. Spatio-temporal variability in fish recruitment to a coral reef. Coral Reefs 12: 105-113.
- Raimondi, P.T. 1990. Patterns, mechanisms, and consequences of variability in settlement and recruitment of an intertidal barnacle. Ecol. Monogr. 60: 283-309.
- Reinboth, R. 1968. Protogynie bei Papagefischen (Scaridae). Z. Naturforsch. 23: 852 - 855.

- coast with tidal currents: complex distribution patterns from a simple model. Mar. Ecol. Prog. Ser. 122: 59-71.
- Roberts, C. M., & R.F.G. Ormond 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar. Ecol. Prog. Ser. 41: 1-8.
- Robertson, D.R., 1988a. Abundances of surgeon fishes on patch-reefs in Caribbean Panama: Due to settlement, or post-settlement events? Mar. Biol. 97: 495-501.
- Robertson, D.R., 1988b. Extreme variation in settlement of the Caribbean triggerfish *Balistes vetula* in Panama. Copeia 1988: 698-703.
- Robertson, D.R. 1988c. Settlement and population dynamics of *Abudefduf saxatilis* on patch reefs in Caribbean Panama. Copeia 1988: 698-703.
- Robertson, D.R. 1990. Differences in the seasonalities of spawning and recruitment of some small neotropical reef fishes. J. Exp. Mar. Biol. Ecol. 144: 49-62.
- Robertson, D.R. 1992. Patterns of lunar settlement and early recruitment in Caribbean reef fish at Panama. Mar. Biol. 114: 527-537.
- Robertson, D.R. 1995. Competitive ability and the potential for lotteries among territorial reef fishes. Oecologia 103: 180-190.
- Robertson, D.R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology 77: 885-899.
- Robertson, D.R., Green, D.G., & B.C. Victor 1988. Temporal coupling of production and recruitment of larvae of a Caribbean reef fish. Ecology 69: 370-381.

territorial Caribbean damselfish *Eupomacentrus planifrons*. Ecology 62: 1162-1169.

Robertson, D.R. & J.M. Sheldon 1979. Competitive interactions and the availability of sleeping sites for a diurnal coral reef fish. J. Exp. Mar. Biol. Ecol. 40: 285-298.

Robins, C.R., Ray, G.C., Douglass, J., & R. Freund 1986. A field guide to Atlantic coast fishes: North America. Houghton Mifflin Co., Boston.

Roughgarden J., Gaines, S & H. Possingham 1988. Recruitment dynamics in complex life cycles. Science 241:1460--1466.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests in the eastern United States. Ecology 62: 1041-0151.

Runkle, J.R. 1982. Patterns of disturbance in some old- growth mesic forests of Eastern North America. Ecology 63: 1533-1546.

Russell, B.C., Anderson, G.R.V. & F.H. Talbot 1977. Seasonality and recruitment of coral reef fishes. Aust. J. Mar. Freshwater Res. 28: 521-528.

Sale, P.F. 1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces; Pomacentridae). Copeia 1971: 324-327.

Sale, P.F. 1972a. Effects of cover on agonistic behavior of a reef fish: a possible spacing mechanism. Ecology 53: 753-758.

Sale, P.F. 1972b. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology 53: 741-744.

Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. *Am. Nat.* 111: 337-359.

Sale, P.F. 1978. Coexistence of coral reef fishes - a lottery for living space. *Env. Biol. Fish.* 3: 85-102.

Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Ann. Rev.* 18: 367-421.

Sale, P. F. 1991a. Introduction. pp. 3-15 *In*: P. F. Sale. The ecology of fishes on coral reefs. Academic Press, San Diego..

Sale, P.F. 1991b. Reef fish communities: Open nonequilibrium systems. pp. 564-598 *In*, The ecology of fishes on coral reefs. edited by P.F. Sale, Academic Press, Inc., San Diego.

Sale, P.F., Douglas, W.A. & P.J. Doherty 1984a. Choice of microhabitats by coral reef fishes at settlement. *Coral Reefs*. 3: 91-99.

Sale, P.F., Doherty, P.J., Eckert, G.J., Douglas, W.A., & Ferrell, D.J. 1984b. Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* 64: 191--198.

Scheltema, R.S. 1974. Biological interactions determining larval settlement of marine invertebrates. *Thalassia Jugoslavia*. 10: 263-296.

Atherinidae). Unpublished Ph. D. Thesis. University of Sydney, Sydney, Australia.

Schmitt, R.J. & S.J. Holbrook 1996. Local-scale patterns of larval supply in a planktivorous damselfish--Do they predict recruitment. Mar. Freshwater Res. 47: 449-63.

Shanks, A.L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311-315.

Shanks, A. L., and Wright, W. G. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. J. Exp. Mar. Biol. Ecol. 114: 1-13.

Shenker, J. M., Maddox, E. D., Wishindki, E., Pearl, A., Thorrold, S. R., & N. Smith 1993. Offshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. Mar. Ecol. Prog. Ser. 98: 31-43.

Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. J. Exp. Mar. Biol. Ecol. 74: 85-109.

Shulman, M.J. 1985a. Recruitment of coral reef fishes: Effects of distribution of predators and shelter. Ecology, 66: 1056-1066.

Shulman, M.J. 1985b. Variability in recruitment of coral reef fishes. J. Exp. Mar. Biol. Ecol. 89: 205-219.

- Recruitment of benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. Mar. Ecol. Prog. Ser. 39: 233-242.
- Shultz, E.T., & R.K Cowen 1994. Recruitment of coral-reef fishes to Bermuda: local retention or long-distance transport? Mar. Ecol. Prog. Ser. 109: 15-28.
- Smith, C.L. 1978. Coral reef fish communities: A compromise view. Envir. Biol. Fishes 3: 109-128.
- Smith, C.L. & J.C. Tyler 1972. Space resource sharing in a coral reef fish community. Bull. Nat. Hist. Mus. L.A. County 14: 125-170.
- Smith, C.L. & J.C. Tyler, 1973. Population ecology of a Bahamian suprabenthic fish assemblage. Am. Mus. Novit. 2528: 1-38.
- Smith, C.L. & J.C. Tyler 1975. Succession and stability in fish communities of the dome-shaped patch reefs in the West Indies. Am. Mus. Novit. 2572: 1-18.
- Sousa, W.P. 1979a. Experimental investigation of disturbance and ecological succession in a rocky intertidal algal community. Ecol. Monogr. 49: 227-254.
- Sousa, W.P. 1979b. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology 60: 1225-1239.
- Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? J. Anim. Ecol. 46: 337-365.

- Barbados, West Indies. Mar. Ecol. Prog. Ser. 133: 13-28.
- Stobutzki, I. C. & D.R. Bellwood 1994. An analysis of the sustained swimming abilities of pre-settlement and post-settlement reef fishes. J. Exp. Mar. Biol. Ecol. 175: 275-286.
- Sundberg, K. & V.S. Kennedy 1993. Larval settlement of the Atlantic Rangia, *Rangia cuneata* (Bivalvia: Mactridae). Estuaries 16: 223-228.
- Sutherland, J.P. 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. Ecology. 71: 955-972.
- Sweatman, H.P.A. 1988. Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. J. Exp. Mar. Biol. Ecol. 124: 163-174.
- Sweatman, H.P.A. 1985. The influence of adults of some coral reef fishes on larval recruitment. Ecol. Monogr. 55: 469-485.
- Tabachnick, B.G, & L.S. Fidell 1989. Using multivariate statistics, 2nd edn. Harper Collins Publishers, Northridge.
- Thorrold, S. R., Shenker, J. M., Maddox, E.D., Mojica, R., & E. Wishinski 1994a. Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. Mar. Biol. 118: 567-578.
- Thorrold, S.R., Shenker, J.M., Mojica, R., Maddox, E.D., & E. Wishinski 1994b. Temporal patterns in the larval supply of summer-recruiting reef fishes to Lee Stocking Island, Bahamas. Mar. Ecol. Prog. Ser. 112: 75-86.

- supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. I. Small-scale distribution patterns. Mar. Biol. 118: 555-566.
- Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. 25: 1-45.
- Thresher, R.E. 1991. Geographic variability in the ecology of coral reef fishes: evidence, evolution, and possible implications. pp. 401--436 *In*, P.F. Sale. The ecology of fishes on coral reefs. Academic Press, Inc., San Diego.
- Thresher, R.E. 1976. Field analysis of the territoriality of the threespot damselfish, *Eupomacentrus planifrons* (Pomacentridae). Copeia 1976: 266-276.
- Thresher, R.E. 1983. Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. Mar. Ecol. Prog. Ser. 10:137-145.
- Thresher, R.E. & E.B. Brothers, 1989. Evidence of intra- and inter-oceanic regional differences in the early life history of reef-associated fishes. Mar. Ecol. Prog. Ser. 57: 187-205.
- Tivy, J. 1992. Historical biogeography. pp. 55-78 *In*: Biogeography: A study of plants and their ecosphere.
- Tolimieri, N. 1995. Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102: 52-63.

- Tomlinen, N. 1998. The relationship between microhabitat characteristics, recruitment and adult abundance in the stoplight parrotfish, *Sparisoma viride*, at three spatial scales. *Bull. Mar. Sci.* 62: *in press*.
- Tupper, M. & W. Hunte 1994. Recruitment dynamics of coral reef fishes in Barbados. *Mar. Ecol. Prog. Ser.* 108: 225-235.
- Underwood, A. J. & E. J. Denley 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. *Ecological communities: conceptual issues and the evidence*. Princeton, N.J., Princeton University Press.
- Underwood, A.J. & P.G. Fairweather 1989. Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* 4: 16-19.
- Victor, B.C. 1986. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecol. Mono.* 56: 145-160.
- Victor, B.C. 1984. Coral reef fish larvae: Patch size estimation and mixing in the plankton. *Limnol. Oceanogr.* 29: 1116-1119.
- Victor, B.C. 1983. Recruitment and population dynamics of a coral reef fish. *Science*. 219: 419-420.
- Warner, R.R. & P.L Chesson, 1985. Coexistence mediated by recruitment fluctuations: A field guide to the storage effect. *Am. Nat.* 125: 769-787.
- Warner, R.R., & S.G. Hoffman 1980. Population density and the economics of territorial defense in a coral reef fish. *Ecology* 61: 772-780.

- Wellington, G.M. 1992. Habitat selection and juvenile persistence control the distribution of two closely related Caribbean damselfishes. *Oecologia* 90: 500-508.
- Werner, E.E., Hall, D.S. Laughlin, D.R., Wagner, D.J., Wilsmann, L.A. & F.C. Funk 1977. Habitat partitioning in a freshwater fish community. *J. Fish Res. Board Can.* 34: 360-370.
- Wiens, J. 1976. Population responses to patchy environments. *Ann. Rev. Ecol. Syst.* 7: 81-120.
- Wilkinson, L., M. Hill, J.P. Welna & Birkenbuel, 1992. *Systat for Windows: Statistics, Version 5* edition Evanston, IL, Systat, Inc.
- Williams, D. M. 1980. Dynamics of the pomacentrid community on small patch reefs in One Tree Lagoon (Great Barrier Reef). *Bulletin of Marine Science* 30: 159-170.
- Williams, D. M., English, S., & M.J. Milicich 1994. Annual recruitment surveys of coral reef fishes are good indicators of patterns of settlement. *Bull. Mar. Sci.* 54: 314-331.
- Williams, D.McB. & P.F. Sale, 1981. Spatial and temporal patterns of recruitment of juvenile coral reef fishes to coral habitats within 'One Tree Lagoon', Great Barrier Reef. *Mar. Biol.* 65: 245-253.

potential movement of planktonic larvae in the central region of the Great Barrier Reef. *Coral Reefs* 3: 229-236

Winer, B.J, Brown, D.R., & K.M. Michels 1992. *Statistical principles in experimental design*. McGraw-Hill, New York.

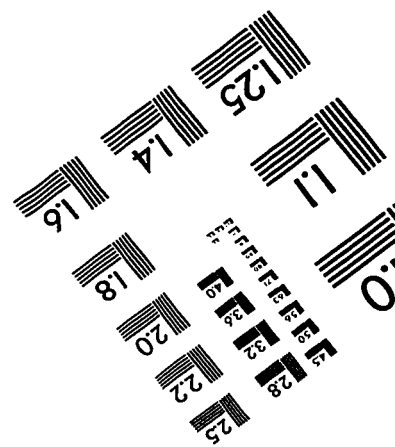
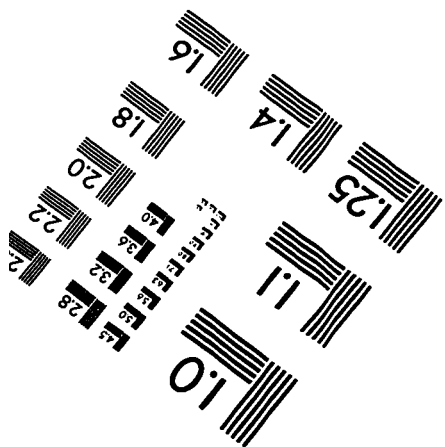
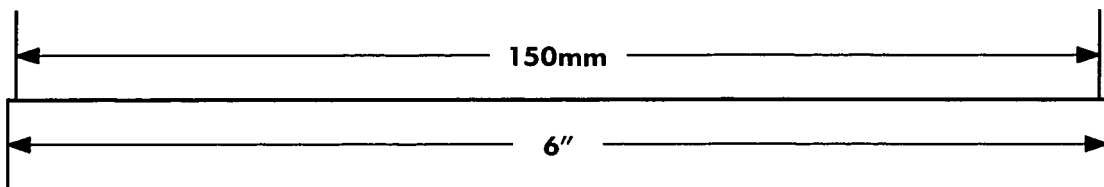
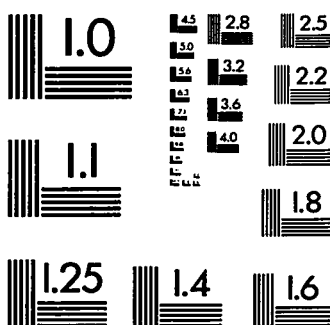
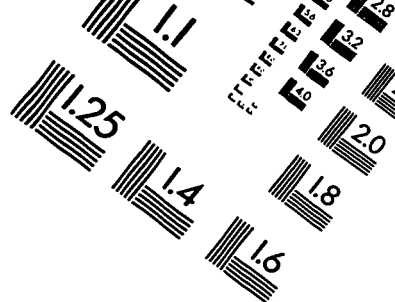
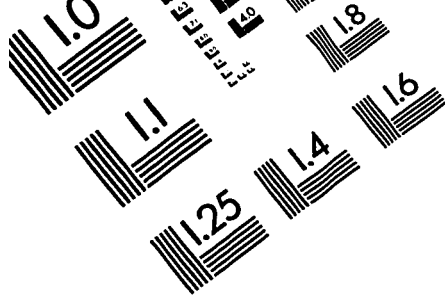
Witman, J.D. 1987. Subtidal coexistence: storms, grazing, mutualism and the zonation of kelps and mussels. *Ecol. Monogr.* 57: 167-187.

Yoshioka, P.M. 1982. Role of planktonic and benthic factors in the population dynamics of the bryozoan *Membranipora membranacea*. *Ecology* 63: 457-468.

Zar, G.H. 1984. *Biostatistical analysis*. 2nd edn. Prentice-Hall, Englewood Cliffs.

Nicholas Tolimieri

Born:	26 May 1969, New York, NY, USA
B.Sc.:	Biology, May 1991, Colby College
Msc.:	Zoology, September 1994, University of New Hampshire
Ph.D.:	Biology, October 1997, University of Windsor



APPLIED IMAGE, Inc
 1653 East Main Street
 Rochester, NY 14609 USA
 Phone: 716/482-0300
 Fax: 716/288-5989

© 1993, Applied Image, Inc., All Rights Reserved